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BULLETIN OF MARINE SCIENCE OF THE GULF AND CARIBBEAN

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THE FLUCTUATIONS OF THE FLORIDA CURRENT¹

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ABSTRACT

Correlations between the annual variations of the drift current of the Straits of Florida, of sea-level, and of the wind stress data are established. The annual march of the sea-level difference between Cat Cay and Miami Beach is computed. It is shown to have a close relation to the annual march of the average charted drift current in the Straits of Florida. The relatively few observations used for these computations are nevertheless shown to be representative. In order to extend the use of the sea-level data, the connection between the S-N component of the mean wind stress in the area of the Florida Straits and the mean sea-level of the same section is studied and a relatively close connection is found. Thus it is shown that, after a proper correction due to the variations of the local wind stress, the sea-level observations at Miami Beach may be used as an index of the year by year fluctuations in the Florida Current.

INTRODUCTION

Since the northeast trades and westerlies, from which the Gulf Stream system obtains its energy, fluctuate in position and velocity with the different seasons of the year, and probably to some extent from year to year, it is generally assumed that this system of water currents similarly fluctuates in strength. The considerable theoretical and practical importance of an accurate knowledge of these fluctuations is well known to oceanographers. For example, Iselin (1938), when reporting on the cooperative investigation of the Woods Hole Oceanographic Institution and the Bermuda Biological Station, writes: "This investigation has as its ultimate goal the solution of the problem of whether or not gradual changes in the strength of the Gulf Stream system have any bearing on the climate and fishery of Great Britain." The existence of annual fluctuations was shown by Montgomery (1938) and Iselin (1940) on the basis of both hydrographic stations and tide gauge records. Later Fuglister (1948) showed that surface

¹ Contribution No. 66 from The Marine Laboratory, University of Miami. These studies were aided by a contract between the Office of Naval Research and the University of Miami.

current observations "... also give what appears to be a consistent picture of annual variations in the current speeds in various segments of the Gulf Stream system." However, variations in volume transport and surface current, in relation to local winds, trade winds, and mean sea-level differences have not yet been studied in continuous detail for the Florida Current.

The present report deals with some of the initial results of recent investigations carried out at Miami. The Cat Cay-Miami Beach section of the Florida Straits is the narrowest portion of the entire Gulf Stream system, the Straits being here restricted between land boundaries about 40 miles apart. For this and other reasons, the above section offers an exceptional opportunity for making detailed and continuous measurement of this part of the Atlantic circulation, for establishing correlations between variations in current and meteorological phenomena.

A necessary preliminary to these ultimate objectives is the determination of the reliability of cross-stream gradients measured by sea-level recordings. Iselin (1940) writes that in order to learn about the effects of long-period variations in the volume of this current, it is first of all necessary to study the annual changes in current pattern and subsurface structure, since annual fluctuations in the transport are greater than the secular changes.² Our computations have confirmed these conclusions and it therefore appears that annual fluctuations may offer an approach to the problem, although available observations are still relatively scarce.

VARIATIONS IN THE SEA-LEVEL DIFFERENCE CAT CAY-MIAMI BEACH

The theory that variations of current across a stretch of open sea are reflected in tide gauge records made on a line normal to the direction of flow must be applied with caution. In the case of the Cat Cay-Miami Beach section, however, it is believed that the strength of the Florida Current compared to that of possible counter-currents and eddies and the good exposure of the tidal stations, together ensure that the effects of purely local water movement on the slope of sea-level are reduced to a minimum. Over this relatively short section it is considered unnecessary to take into account the variations in atmospheric pressure between the two stations.

² In this connection it is worthwhile to mention that apparently the main part of the year to year rising of the mean sea-level at Miami Beach since about 1930, as shown by Iselin (1940), depends upon either the absolute or relative sinking of the Atlantic coast of the United States (cf. Marmer, 1948) and not upon a weakening of the Florida Current.

The monthly means of sea-level which are available from Cat Cay are given in Table I. The data are reduced to mean sea-level during the observation period. Similar means of the tide gauge records from Miami Beach are given in Table II. From Tables I and II the variation

TABLE I
MONTHLY MEANS OF SEA-LEVEL IN CAT CAY IN CM.
REFERRED TO THE MEAN SEA-LEVEL DURING 1938-41.³

	J	F	M	A	M	J	J	A	S	O	N	D
1938	..	..	-3.9 ¹	-3.9	-3.6	-0.8	2.0	4.1	7.0	4.8	-1.1	-6.2
1939	-7.8	-6.2	-1.7	0.1	-0.4	3.4	6.0	7.3	10.4	7.3	-5.8	-5.3
1940	-10.2	-10.9	-7.2	-7.1 ²	1.7	-1.1	1.3	8.2	12.1	7.9	4.1	0.1
1941	-5.0	-0.1	..	..	..	..	..	..	..	..	..	..
Mean	-7.7	-5.7	-4.2	-3.6	-0.8	0.5	3.1	6.5	9.8	6.7	-0.9	-3.8

¹ 28 days' average

² 20 days' average

TABLE II
MONTHLY MEANS OF SEA-LEVEL AT MIAMI BEACH IN CM. REFERRED TO THE
MEAN SEA-LEVEL FROM 1938 MARCH TO 1941 FEBRUARY.³

	J	F	M	A	M	J	J	A	S	O	N	D
1938	..	..	-10.3	-8.1	-4.2	-5.6	-9.4	-2.9	3.5	15.0	16.9	1.6
1939	-7.2	-9.0	-10.0	-6.9	-0.5	-3.9	-5.6	-0.2	14.1	18.7	14.5	-5.3
1940	-5.6	-6.9	-7.5	-12.7	-2.1	-7.5	-5.1	5.7	14.5	20.2	2.9	0.1
1941	3.8	3.5	..	..	..	..	..	..	..	..	..	..
Mean	-3.0	-4.1	-9.3	-9.2	-2.3	-5.7	-6.7	0.9	10.7	18.0	11.4	-1.2

in the sea-level difference between Cat Cay and Miami Beach may be computed with reference to the mean value of the difference. However, it is desirable to obtain at least an approximate average value for the absolute difference in height between these stations. We have made use of the formula, (Sandström, 1903):

$$\Delta H = \frac{2 \Omega \sin \varphi}{g \varphi} l v \quad (1)$$

where ΔH is the height difference, Ω the angular speed of the earth, φ the mean latitude of the section in question, $g \varphi$ the acceleration of gravity, l the breadth of the current, and v the mean surface velocity of the current. This formula is, *a priori*, valid only when considering steady and frictionless currents. However, as pointed out by several previous authors, it must also be valid to a certain degree in the Straits of Florida. From Pillsbury's observations during March to May, 1890, the corresponding average height difference between Gun Cay and Miami Beach during that period was calculated to be 58 cm. By applying this absolute height difference to the tide data for the corresponding period it is possible to derive absolute height differences for

³ Calculated from tidal data kindly supplied by the U. S. Coast and Geodetic Survey.

TABLE III
MONTHLY MEANS OF THE SEA-LEVEL DIFFERENCE
BETWEEN CAT CAY AND MIAMI BEACH GIVEN IN CM.

	J	F	M	A	M	J	J	A	S	O	N	D
1938	..	..	60.4	58.3	54.6	58.9	65.3	61.0	57.4	43.7	36.0	46.1
1939	53.4	56.8	62.3	61.0	54.0	61.4	65.6	61.4	50.4	42.5	33.9	54.0
1940	49.5	50.1	53.7	59.5	57.7	60.4	60.4	56.5	51.6	41.5	55.2	54.0
1941	45.2	50.4	..	..	..	..	..	..	..	..	..	..
Mean	49.4	52.4	58.8	59.6	55.4	60.2	63.8	59.6	53.1	42.6	41.7	51.4
Computed Differences	52.2	56.1	58.2	60.1	57.7	62.2	63.0	57.3	49.5	40.6	40.2	50.0

each month. The average of these was found to be 54 cm., which agrees closely with 55 cm. computed by Iselin (1940).

Using 54 cm. as the average difference in height, the annual march in sea-level difference between Cat Cay and Miami Beach is given in Table III and Figure 1. The most characteristic features of this are

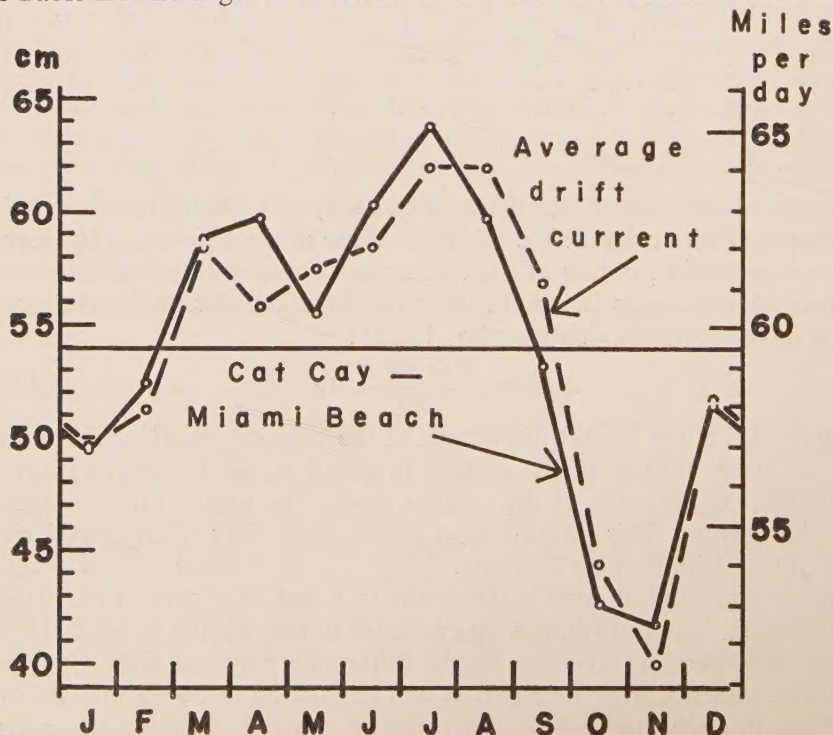


FIGURE 1. Annual march of the difference in sea-level at Cat Cay and Miami Beach (solid line), compared with the average drift current (dashed line).

the maximum in July which is followed by a rapid fall to the minimum in November. A secondary maximum occurs in April and a secondary minimum in May. A similar seasonal cycle was found by Montgomery (1938) for the flow between Charleston and Bermuda. Iselin (1940) deduces a similar cycle from the tide gauge observations at Cat Cay and at Miami Beach during the period 1938 April to 1939 December.

AVERAGE DRIFT CURRENT

We may now compare the variations mentioned with the annual cycle of the average charted drift current⁴ in the Straits of Florida given in Table IV. The following considerations must, however, be taken into account:

(1) The average drift currents are related only to the surface current.

(2) It is obvious that the charted average drift current in the Florida Straits, owing to the unique location of the most frequently used ship routes, is lower than the maximum current and probably lower than the average surface current of the whole section.

(3) The sea-level differences, as pointed out also by Montgomery (1941 b), seem to correspond to the mass transport over a certain depth: "The computed difference of sea-level across the Straits shows little correlation with the computed transport. The sea-level difference is, however, seen to be closely correlated with the transport of water having anomaly of specific volume greater than 300 cl. ton⁻¹ (warmer than about 23°C.) or greater than 200 cl. ton⁻¹ (warmer than about 19.2°C.)"

TABLE IV
AVERAGE DRIFT CURRENT IN THE FLORIDA STRAITS
(IN NAUTICAL MILES PER DAY)

J	F	M	A	M	J	J	A	S	O	N	D	Mean
57.0	57.7	62.0	60.5	61.5	62.0	64.0	64.0	61.2	54.0	51.5	58.2	59.5

The similar course of both of the elements (Figure 1) in question is rather evident. Although the relationship seems to be parabolic⁵ it is permissible to check the linear correlation since the records occur

⁴ The annual cycle of the Florida Current computed by Fuglister (1948) from the "Current Atlas of the North Atlantic Ocean," H. O. Misc. 10,688 (1946) is approximately the same as given in Table IV.

⁵ The relationship between them does not seem to be linear but parabolic:

$$\Delta H = 0.0152 v^2$$

where ΔH is given in cm. and v in nautical miles a day.

only in a narrow portion of both of the coordinates. The correlation coefficient between them is

$$r = \frac{\sum (\Delta H \times v)}{\sum (\Delta H)^2 \times \sum v^2} = +0.95 \quad (2)$$

or, taking into consideration that the number of values under comparison, n , is only 12,

$$r' = \sqrt{1 - \frac{n-1}{n-2} (1-r^2)} = +0.94. \quad (2')$$

At the same time the probable error of the coefficient is

$$F = \pm 0.6745 \frac{1 - (r')^2}{\sqrt{n}} = \pm 0.02, \quad (3)$$

so that the relation $|r'/F|$ is approximately 41 which indicates a very intimate connection indeed (Conrad, 1950).

REPRESENTATIVITY OF OBSERVATIONS OVER A PERIOD OF THREE YEARS ONLY

Our next task is to check the representativity of the sea-level observations performed during the short period of three years. The only way is to compare the Miami Beach sea-level records during the period from 1938 March to 1941 February with the corresponding records during the period from 1931 June to 1949, excluding from the latter the records of the former. The correlation coefficient between them is $r' + F = +0.94 \pm 0.02$ and hence the relationship $|r'/F| = 37$. This high degree of significance strongly suggests that the observations used are representative.

SEA-LEVEL OBSERVATIONS AT MIAMI BEACH

In order to extend the use of the sea-level data, the correlation coefficient is computed for the connection between the sea-levels at Miami Beach and the sea-level differences between Cat Cay and Miami Beach. From the records of the 36 months available, the following indication of a close connection is obtained: the correlation coefficient $r + F = -0.78 \pm 0.04$ and the relation $|r/F| = 18$. The average relationship between the two quantities mentioned is

$$\Delta H = -0.66 \underset{\text{MB}}{H} + 54.0. \quad (4)$$

This equation shows that the variations at Miami Beach are, on an

average, three times those of Cat Cay. In addition, it shows that the mean monthly variation from mean sea-level at the two stations does not in general move in opposite directions as would be expected if the variations in the sea-level were solely due to fluctuations in the Florida Current. Somewhat similar conclusions were drawn by Iselin (1940).

Since the above relationship (4) is only an average one, the sea-level records of Miami Beach must contain not only the influence of the sea-level difference between Cat Cay and Miami Beach, indicating fluctuations in the Florida Current, but also an influence of the local wind stress. This local influence can be obtained by subtracting from the actual monthly means of sea-level at Miami Beach the theoretical means of the same sea-level derived from the equation (4). The actual and theoretical monthly means and their difference, D , derived in this manner are given in Table V. In the last row of the same table the

TABLE V
ANNUAL MEANS OF THE SEA-LEVEL AT MIAMI BEACH
AND THE S-N COMPONENT OF THE MEAN WIND STRESS

	J	F	M	A	M	J	J	A	S	O	N	D
Actual												
Means	-3.0	-4.1	-9.3	-9.2	-2.3	-5.7	-6.7	0.9	10.7	18.0	11.4	-1.2
Theoretical												
Means	6.9	2.4	-7.2	-8.4	-2.1	-9.3	-14.7	-8.4	1.4	17.2	18.5	3.9
Difference,												
D	-9.9	-6.5	-2.1	-0.8	-0.2	3.6	8.0	9.1	9.3	0.8	-7.1	-5.1
Mean Wind Stress,												
τ_y	48	-24	-34	-19	-3	14	15	10	0	-31	-67	-56

S-N component of the mean wind stress, τ_y in 10^{-2} dynes cm^{-2} in the area of 20° - 30° N., 75° - 80° W. is also given.⁶ The variable D , of course, represents the changes in mean sea-level of the entire section compared with hypothetical values of it derived from the assumption that the changes were solely due to fluctuations in the Florida Current. There must be a close connection between the local wind stress and the variable, D . The correlation coefficient between D and the S-N component of the wind stress, τ_y in the area west of Florida peninsula is $r' + F = +0.83 \pm 0.06$ and the relation $|r'/F| = 14$. This apparently close connection seems to show that the portion of the actual sea-level variations not indicated by theoretical monthly means, i.e., not due to the fluctuations in the Florida Current, must be due to the local wind stress, especially the S-N component of it, in the area of the

⁶ These wind stresses and several other similar computations for our purposes were made by Mr. Stanley E. Asplund on the basis of the SIO report No. 21.

Straits of Florida. A similar "striking agreement" was found by Montgomery (1938) between the annual cycles of (a) percentage frequency of net "onshore" winds at Savannah and (b) annual variation of sea-level at Charleston.

The method of least squares gives as linear relationship

$$D = 0.20 T_y + 3.9.$$

These corrections are applied to the actual monthly means of Miami Beach sea-level. The theoretical sea-level differences between Cat Cay and Miami Beach are then computed from the corrected means using equation (4). The sea-level difference values thus obtained are in relatively close agreement with the actual values (cf. last line in Table III). This fact shows that it is possible to use the sea-level observations at Miami Beach as an index of the year by year fluctuations in the Florida Current.

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A REVIEW OF THE CRUSTACEAN GENUS *STILBOGNATHUS* VON MARTENS (DECAPODA, MAIIDAE) WITH DESCRIPTION OF A NEW SPECIES FROM THE EAST COAST OF FLORIDA¹

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ABSTRACT

The occurrence of the genus *Stilbognathus* is reported for the first time in American waters with the description of a new species, *S. burryi*, from the unique female holotype taken off Hillsboro Light, Florida, in 125 feet of water, by L. A. Burry. A key to the known species of *Stilbognathus* is given and the relationships of the five genera representing the subfamily Ophthalmiinae in the western Atlantic are considered.

INTRODUCTION

A *Tyche*-like spider crab found among dredgings obtained off the east coast of Florida in 1946 has proved to be generically as well as specifically distinct from *T. emarginata* White (1847) of the tropical western Atlantic, and is herein assigned to *Stilbognathus* von Martens. Since the genus is new to the Western Hemisphere, its description is given below for the benefit of American workers, together with a description of the new species and a key to the existing ones.

The discovery of *Stilbognathus* in the western North Atlantic brings to five the number of maiid genera having certain remarkable characters in common which call for their recognition as a distinct element in the American crustacean fauna. For this purpose the system of classification proposed for the Maiidae by Balss (1929) has definite advantages over the more familiar system adopted by Rathbun (1925) and will be followed in this paper.

Illustrations are from the pen of Anker Petersen, staff artist, Allan Hancock Foundation.

Subfamily OPHTHALMIINAE Balss

Stenocionopiinae Miers, 1879, p. 652.

Stenocionopoida Alcock, 1895, p. 161, p. 166.

Ophthalmiinae Balss, 1929, p. 6. (Name substituted for *Stenocionopiinae* Miers to conform with the substitution of *Ophthalmias* for *Stenocionops* [Rathbun, 1897, p. 157]).

¹ Contribution No. 88 from the Allan Hancock Foundation.

The orbit consists, if complete, of a supraocular eave and a postocular spine, while the intercalated spine is lacking; on this account the subfamily has no relation to the Maiinae [as restricted by Balss], in which the intercalated spine is present. Longer spinuous outgrowths on the supraocular eave and on the postocular spine are for the most part present. The shape of the body is elongate, somewhat truncate in front, often provided behind with a median spine or outgrowth. (Balss)

The American genera belonging to this subfamily, as recognized by Balss (*op. cit.*), are *Picroceroides* Miers (1886), *Pitho* Bell (1835), *Tyche* Bell (1835), and *Thersandrus* Rathbun (1897: name substituted for *Sisyphus* Desbonne). The remaining genera, including *Stilbognathus* von Martens (1866), are, or until now have been, restricted to the Old World. *Picroceroides* (one species: *P. tubularis* Miers, from Fernando Noronha and Bahia, Brazil) is related to *Picrocerus* A. Milne Edwards, New Caledonia, and together with *Ophthalmias* Rathbun (1897) (= *Stenocionops* Latreille partim), West Africa, India, and Hawaii, forms group one of Balss. *Pitho* (10 species: three Pacific, seven Atlantic) and *Thersandrus* (one species: *T. compressus* [Desbonne], from Guadeloupe) are joined with *Cyclocoeloma* Miers (1880), Amboina, in a second group. To quote directly: "The two genera *Tyche* Bell (1835) and *Stilbognathus* v. Martens (1886) form a third group which show their especially close relationship through the remarkable structure of their third maxillipeds. Of them *Tyche* (two species: *T. lamellifrons* Bell, California², and *T. emarginata* White, Antilles) is the more primitive, since it yet possesses seven free abdominal segments; supraocular eave and postocular spine are broadened lamella-like and lie against one another, but remain separated through a narrow slit. A strong preocular spine is present. From this genus *Stilbognathus* (three species: *S. tycheformis* Bouvier [1915], Mauritius; *S. erythraeus* v. Martens [1866], Red Sea; and *S. martensii* Miers [1844], Providence Island) may be derived. Here the fusion of the postocular spine with the supraocular eave, initiated in *Tyche*, is culminated; in the case of [*S.*] *tycheformis* the former may still be differentiated clearly, while in the other two species it no more stands out separately. The abdomen shows fusion of segments 4 to 6 in the female." Balss also recognizes a fourth group consisting of the single genus *Criocarcinus* Milne Edwards, Andamans and New Caledonia. All four he holds to have arisen from the primitive genus

² *Lapsus calami*. The type locality of *T. lamellifrons* is clearly Panama.

Pseudomicippe Heller, Red Sea, Ceylon, and Salam Sea, which he relates to *Naxia* Latreille of the Inachinae.

GENUS *Stilbognathus* VON MARTENS

Stilbognathus von Martens, 1866, p. 379. (Type species: *S. erythraeus* von Martens.) Bouvier, 1915, p. 248.

The second segment [of the maxilliped] shows on its outer half a deep, strongly elliptical groove, which is intermittently set with setae; its inner margin carries a row of horizontal setae and behind these stronger teeth . . . The insertion of the third into the second segment describes a great curve, in that the third segment itself is inserted wide and deep and the second invades with a capitate projection, so that the whole can be compared to a cross section of a human hip joint . . . Finally, *the third segment is strongly arched, brilliantly glistening and white, as if overlaid with enamel.* [Italics author's] However, its upper outer corner is flat and appears as a special, alate piece. (von Martens)

The postorbital lobes are totally lacking; one part of the joints of the basal antennal article is visible; the buccal cavity is enlarged behind and before, less, however, than in the case of *Stenocionops* [= *Ophthalmias* Rathbun], especially at its anteroexternal angle where nevertheless its margin is elevated in a strong rim; into this angle penetrates the corresponding expansion of the merus [of the external maxilliped], which is of moderate size; on the other hand the merus is very much developed on its inner border, where it presents anteriorly a slight notch; it is articulated rather distantly posteriorly on the external border of the ischium so that the latter article makes a great rounded advance on the merus; the inferior surface of the two articles is not as rugose as in [*Stenocionops* and *Tyche*], but smooth and porcellanic (from which the name that has been given to the genus); the longitudinal depression of the ischium is large and deep, but shorter, however, than that of *Stenocionops*. The three anterior abdominal segments and the telson present distinct and mobile articulations. (Bouvier)

To the genus thus characterized, Bouvier (1915, p. 252) added a species with a postorbital horn, which he designated *S. tycheformis* to indicate that it possessed the glistening maxillipeds of *Stilbognathus* and the postorbital lobe of *Tyche*. It is in a like sense that the following species is linked to those of von Martens and of Miers, although, as in the case of Bouvier's species, the erection of a new genus might be justified.

A KEY TO THE SPECIES OF *Stilbognathus*

- 1a. Postorbital horn absent, posterior projection of carapace a single median lobe
 - 2a. Merus of external maxilliped strongly arched, its outer corner alone flat and alate; notch on inner margin opposite articulation of palpus without a tooth or lobe
erythraeus v. Martens (1866)
 - 2b. Merus of external maxilliped flattened, its anteroexternal angle produced and acute; notch on inner margin opposite articulation of palpus provided with a tooth or lobe
martensii Miers (1884)
- 1b. Postorbital horn present, posterior projection of carapace bi- or trilobate
 - 3a. Postorbital excrescence lobiform, well separated from preorbital horn and only half the length of eyestalk. Posterior projection of carapace trilobate, median lobe most protuberant. Merus of external maxilliped depressed and transversely sulcate
tycheformis Bouvier (1915)
 - 3b. Postorbital excrescence lamelliform, touching preorbital horn along a closed fissure, and equaling length of eyestalk. Posterior projection of carapace weakly bilobate. Merus of external maxilliped smooth and rounded
burryi, n. sp., p. 252

Stilbognathus burryi, NEW SPECIES

Plate 1, Figures 1-6

Type: Ovigerous female, holotype, from $1\frac{3}{4}$ miles East Northeast of Hillsboro Light, Florida East Coast, June 5, 1945, 125 feet, hard rock, broken shell, collected by L. A. Burry at Hancock Foundation station A73-45 (=Burry station 41). Type deposited in the collections of the Allan Hancock Foundation, Los Angeles, California, No. 451.

Measurements: Holotype female, length 20.8 mm., length posterior to gastric summit 12.5 mm., width opposite postbranchial tubercles 13.8 mm., exorbital width 11.6 mm., rostrum 2.3 mm., width 3.3 mm., cheliped 13.6 mm., chela 5.5 mm., dactyl 2.3 mm., height of palm 1.5 mm., legs 22.6, 17.7, 14.9, and 12.2 mm., respectively.

Diagnosis: Rostral horns short, lobate, well separated from preorbital, which are acute and incurving. Gastric region high, swollen; cardiac region similarly prominent. Anterior and posterior branchial

EXPLANATION OF PLATE

PLATE I

Stilbognathus burryi, new species (p. 252)

Female holotype

FIGURE 1. Dorsal view, x 2.6

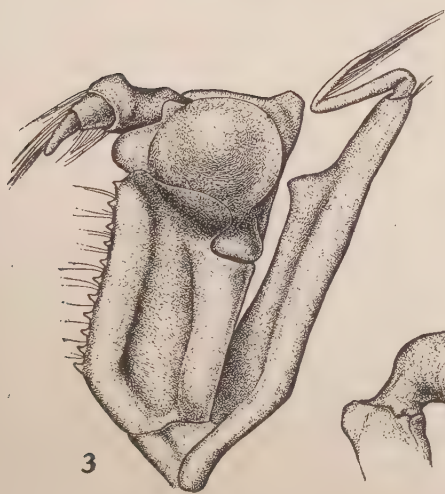
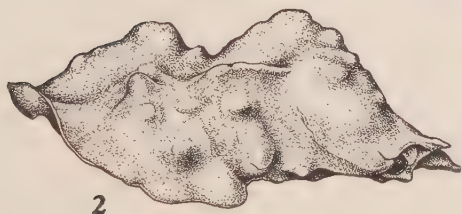
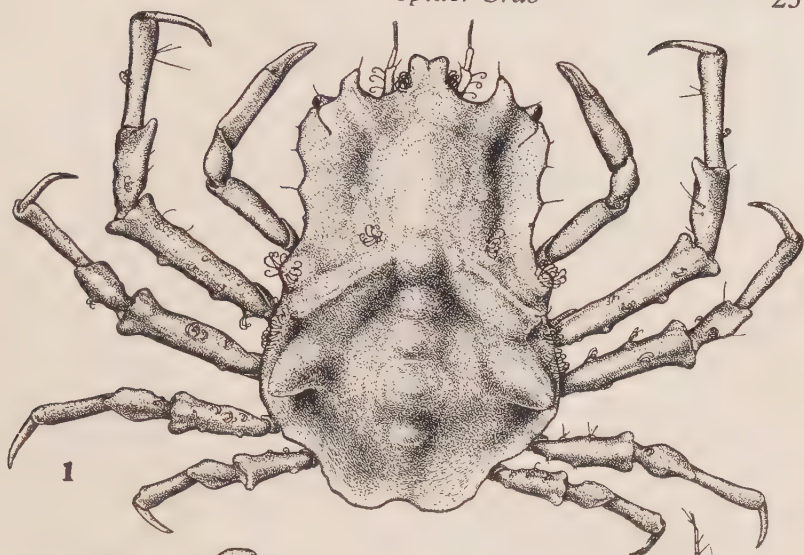
FIGURE 2. Right lateral view, x 2.6

FIGURE 3. Left outer maxilliped, x 12.7

FIGURE 4. Ventral view of orbit, x 5.3

FIGURE 5. Abdomen, x 3.2

FIGURE 6. Right chela, x 7.4



prominences discontinuous. Orbit commencing beneath, the exorbital tooth forming a shallow cup into which the eye is partially retractible. Merus of external maxilliped hemispherical, glistening; ischium longitudinally sulcate, exognath with basal projection directed posteriorly.

Description: Carapace roughly rectangular in outline, high and irregular in profile; six prominent elevations, two anterobranchial (paired), two post-branchial (paired), one cardiac, and one gastric; greatest width of carapace at postbranchial level. Rostrum small, composed of two lobate horns fused in midline, anterior margins broadly arcuate, outer margins subparallel or slightly diverging, a tuberculate ridge surmounted by a cluster of hooked hairs at base of each. Preorbital horns separated from rostral by a broad saddle, inner margins recurving, tips acute, hair-tipped, falling considerably short of rostrum, outer margins broadly arching. Postorbital lobe meeting preorbital along a closed fissure but projecting slightly beyond and beneath it to form a commencing orbit which completely conceals the retracted cornea from dorsal view. Gastric region elevated, swollen, topped by a large, blister-like tubercle preceded by a smaller tubercle, in advance of which are four low tubercles in horizontal line. Gastric region declivitous anteriorly, rounding off laterally into the narrowed and concave hepatic areas. Cardiac region completely separated from gastric, to which it is similar but less elevated, and consisting of a large, rounded tubercle in advance of which is a single small granule, similar granules or low tubercles laterally and posteriorly outlining a diamond of which the cardiac tubercle is the center. Anterior branchial ridge short and acute, continuous with sides of gastric elevation, and bearing a hair-set tubercle on its outer slope. Posterior branchial prominence triangular in outline, bluntly pointed, and separated from the anterior branchial by a low depression, external to which occurs a sharp tubercle on the side of the carapace, which is widest at this level. Posterior border extended as two thin, rounded lobes with crenulate, upturned margins.

Basal antennal article very broad, a short projection internally, a more extensive ridge externally consisting of three swellings in line, the most advanced being the anteroexternal projection. Eystalks short and thick, exposed in a broad V made by the outer margin of the basal antennal article and the exorbital tooth, which forms a shallow cup into which the cornea is partially retractible. Antennules small and deeply recessed behind a strong, posteriorly directed inter-antennular spine. External maxilliped with two deep, parallel grooves,

the internal one entirely within the ischium, the external one formed by the outer border of the ischium and the excavate inner border of the exognath, the basal projection of which does not recurve to enter the groove of the ischium, as in *Tyche*, but continues posteriorly and medially to the triangular median sternite. Merus of maxilliped inserting deeply into outer border of ischium, central portion a glistening white hemisphere onto the lower slope of which the ischium advances boldly, anteroexternal portion a thin, triangular blade, anterointernal portion doubly notched to receive the flattened palp, the first segment of which has a bilobate margin. A tubercle on either side of buccal area, the external angles of which are broadly rounded and strongly rimmed.

Cheliped of female more slender than first walking leg and considerably shorter; merus roughened, a median tubercle externally and a proximal and median tubercle in a diagonal line beneath; carpus roughened but non-tuberculate; manus becoming smoother distally, upper and lower margins subparallel; fingers slender, attenuated, meeting without gape, edges denticulate. First ambulatory leg much the longest, remaining members decreasing rapidly in length; merus of leg one with a row of four or five small tubercles above and two or three larger tubercles on outer border, a blunt upper distal spine, meri of remaining legs with reduction in number and size of tubercles proportional to their respective lengths; carpus of leg one with a median tubercle above and a distal spine more prominent than that of the merus, carpi of remaining legs with terminal spine reduced or wanting; propodi cylindrical, unarmed, widening distally; dactyli long, slender, falciform, a hair-tipped denticle basal to nail of each.

Female abdomen almost circular in outline, segments 4-6 fused.

The male of the species is unknown.

Remarks: In addition to the remarkable maxilliped and the five-segmented abdomen, which immediately set it apart from *Tyche*, the new *Stilbognathus* possesses a high profile with prominent gastric and cardiac tubercles and a divided branchial ridge suggestive of *Lissa*, rather than the *Tyche*-form carapace, which is flattened and leaf-like.

The finding of a new species of *Stilbognathus* off the Florida East Coast brings still another Old World genus to American shores and indicates a more general circumtropical distribution of the Ophthalmiinae than heretofore recognized.

I take great pleasure in naming this distinctive species for my good

friend and former neighbor, Mr. L. A. Burry, conchologist, of Pompano Beach, Florida.

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PHOSPHORUS EXCHANGE IN A SUB-TROPICAL MARINE BASIN¹

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ABSTRACT

The phosphorus concentration of the sediment and overlying water of a shallow marine basin in Biscayne Key, Florida was determined periodically during 1950 and 1951 for the purpose of detecting any phosphorus exchange taking place between the sediment and water. The phosphorus in the sediment was shown to decrease in the summer, accompanied by an increase in the water phosphorus. Exactly the opposite effect was observed during the winter months. Observations of the pH of the sediment and water disclosed that transfer of phosphorus from sediment to water was accompanied by a slight decrease in pH.

INTRODUCTION

The mechanism of the regeneration of inorganic phosphorus in the open sea is well known in its more general aspects. Waksman and Hotchkiss (1938) showed that most of the decomposition of nitrogenous organic matter takes place during the descent to the ocean floor. Since phosphate and nitrate are utilized and regenerated in a fairly constant atomic ratio, most of the particulate organic phosphorus is probably also regenerated before it reaches the bottom in the open sea. In shallow inshore waters, however, there is a possibility that a significant amount of regeneration takes place in the sediment as well as in the water above it. If such a phenomenon exists, it is desirable to know to what extent the regenerated phosphate is transferred back to the water, and the manner in which physical and chemical conditions modify this transfer.

Hayes and Coffin (1951) recently conducted a study of the exchange of nutrients in Bluff Lake, Nova Scotia. Radiophosphorus was introduced onto the surface of the lake, in which complete mixing occurred, and analyses of surface and bottom water were made at frequent time intervals. The surface and bottom waters reached equality of concentration within a few days, after which there was a steady decline, approximately seven per cent of the radio-phosphorus disappearing from the water each day. It has been suggested by Hayes and Coffin that an equilibrium exists between the mud,

¹ Contribution No. 67 of The Marine Laboratory, University of Miami.

plants and zooplankton on one hand, and the water on the other. If the mud and living forms contained many times as much phosphorus as the water, and if equilibration between them were rapid, any added material would disappear rapidly from the water.

It is desirable to know if an equilibrium similar to the one described above also exists in a marine environment. A preliminary study was therefore made in order to investigate the relationship existing between the phosphorus in sediment and that in the overlying water in a sub-tropical inshore marine environment off southern Florida. The investigation was part of a broader survey of ecological conditions at Hurricane Harbor. The topography of the harbor and the specific reasons for choosing it as the site for the survey will be discussed in detail by W. S. Shoemaker in a forthcoming article covering the remainder of the survey.

The author wishes to express his gratitude to Mr. Shoemaker for allowing the use of some of his field data, and to Dr. Hilary B. Moore for his advice. This article is part of a thesis submitted as one of the requirements for the degree of Master of Science at the University of Miami, Florida.

METHODS

The sampling sites for the investigation consisted of two stations in Hurricane Harbor, Biscayne Bay, Florida. Twelve sampling operations at approximately monthly intervals were conducted at each station, beginning in June, 1950. The harbor is a "Y" shaped inlet in Biscayne Key (Figure 1), sheltered from wind and wave action on three sides by the key, and opening on the western side into Biscayne Bay. A narrow channel three meters deep is cut through a very shallow shelf which would otherwise block the harbor entrance. The water in the harbor is similar to that in the bay proper in that it undergoes more radical seasonal changes in physical properties than typical off-shore water due to its comparative isolation and its shallow depth.

In order to study the relationships discussed above, it was necessary to report results of analyses in comparable units. Components of soils and sediments are usually reported on a weight/weight basis, while trace elements in sea water are normally determined on a weight/volume basis. The weight/volume relationship was selected for this experiment since the author was primarily interested in de-

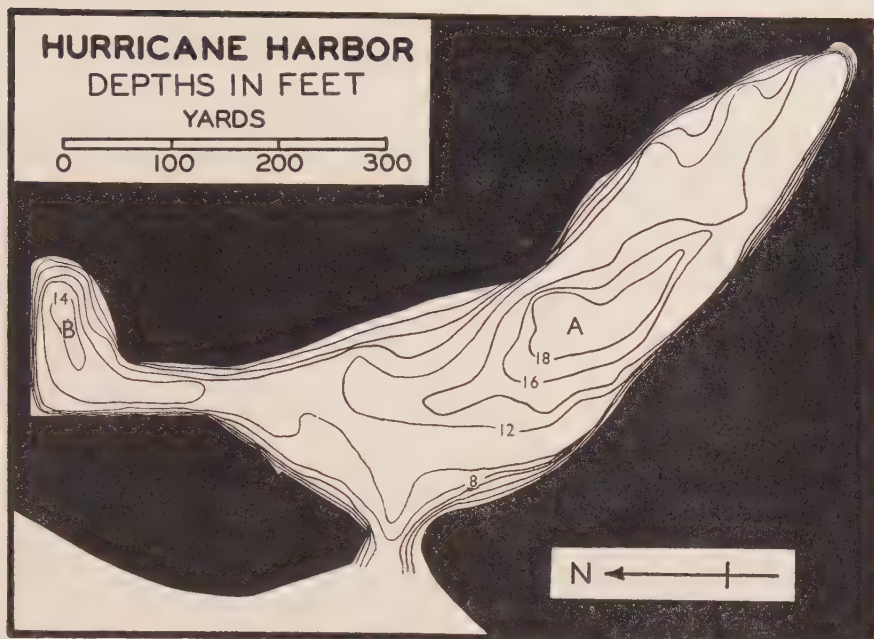


FIGURE 1. Bathymetric chart of Hurricane Harbor (prepared by W. S. Shoemaker and H. B. Moore), showing location of stations.

termining the phosphorus exchange taking place between a sector of sediment and the column of water above it.

At station B3 on September 4, 1950, a diver obtained core samples of sediment 15 cm. in diameter and from 5-25 cm. in length. These cores were used for the determination of the volume *in situ* of one gram of dry sediment. The average volume for 14 samples was 2.05 ml. From this it follows that:

$$\text{gram-atoms P/M}^3 = \frac{\% \text{ P}}{2.05} \times \frac{10^4}{30.98}$$

Water samples were taken at meter intervals at each station. Sediment samples were taken with an Ekman grab which penetrated the sediment to a depth of approximately five centimeters. Whenever possible, sampling operations were carried out at a high tide in order to have a water column of maximum, uniform height. The date and tide data at each station are recorded in Table I.

The method of Redfield *et al.* (1937) was used for estimation

TABLE I
DESCRIPTION OF STATIONS

<i>Station</i>	<i>Date</i>	<i>Tide</i>
A1, B1	June 28, 1950	2/3 flood
A2, B2	July 24, 1950	high
A3, B3	Sept. 4, 1950	high
A4, B4	Sept. 26, 1950	2/3 flood
A5, B5	Oct. 12, 1950	2/3 flood
A6, B6	Nov. 11, 1950	1/2 flood
A7, B7	Dec. 16, 1950	high
A8, B8	Jan. 22, 1951	2/3 flood
A9, B9	Feb. 25, 1951	1/3 ebb
A10, B10	Mar. 17, 1951	high
A11, B11	Apr. 14, 1951	high
A12, B12	June 2, 1951	2/3 flood

of total phosphorus in the water samples, with the exception that three drops of 30 percent hydrogen peroxide were used to oxidize the organic matter remaining after digestion with sulfuric acid.

Essentially the same colorimetric procedure was used for analysis of the sediments as was used on the water samples. The sediment was dried at 105° C. and samples weighing 100 milligrams were digested with sulfuric acid, then oxidized with hydrogen peroxide. The samples were diluted and centrifuged. The supernatant liquid and washings were diluted to 200 ml., and 50 ml. aliquots were taken from this. Acid solutions of ammonium molybdate and stannous chloride were added, and the color of the solution was compared with that of standards. A Fisher Electrophotometer with a 650 $m\mu$ filter attachment was used for all colorimetric determinations in this investigation.

Four samples of sediment were taken from different sections of the harbor and analysed for total phosphorus by the method just outlined. To verify the accuracy of the method, the samples were also analysed according to the method suggested by the Association of Official Agricultural Chemists (1945) for the volumetric determination of total phosphorus in soils. In each of the four pairs of analyses, the results of the colorimetric analysis deviated from that of the accepted volumetric method by less than 3.5 per cent.

The salinity of the water samples was determined volumetrically by titration of the sample with silver nitrate solution, using the Knudsen apparatus. Temperature measurements were made immediately after sampling, using a precision thermometer graduated in tenths of a degree Centigrade. Since the depth at the deep station

was only six meters, the change in temperature in the time lapse between sampling and measurement was negligible.

pH measurements were made on the sediment and water samples, immediately after sampling, with a Beckman Model G pH Meter. The sediment was so soft that the standard type glass and calomel electrodes could be immersed in it without danger of damage.

RESULTS

Water temperatures at Hurricane Harbor were found to decrease with depth. The difference between surface and bottom temperatures varied from 0.5° to $5^{\circ}\text{C}.$, depending upon the season. The greatest seasonal range in temperature was at the surface, where the variation from summer to winter was almost $12^{\circ}\text{C}.$ as compared to a variation of less than $9^{\circ}\text{C}.$ at a depth of six meters.

At every station the salinity of the water was found to increase very slightly with depth. The salinity was high in the summer and low in the winter, with a much wider seasonal variation than would be encountered in offshore water. Sigma-t values were computed from the water salinities and temperatures. These values, plotted in Figure 2, show a high degree of stratification existing in the harbor at all times. Sigma-t curves are shown here only for Station A because

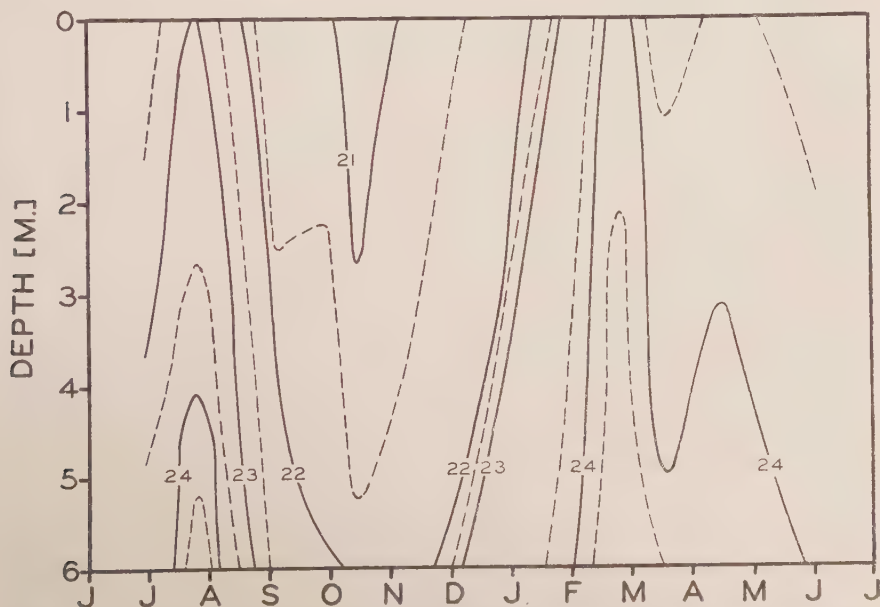


FIGURE 2. Seasonal variation in the density (sigma-t) of water at Station A.

density determinations at both stations gave results which agreed very closely.

The pH of the water at both stations usually showed a maximum in the first meter, followed by a gradual decrease to the bottom. There was no significant seasonal variation in pH in the surface water, but near the bottom and in the sediments, there was a measurable maximum in winter and a minimum in summer (Figure 3).

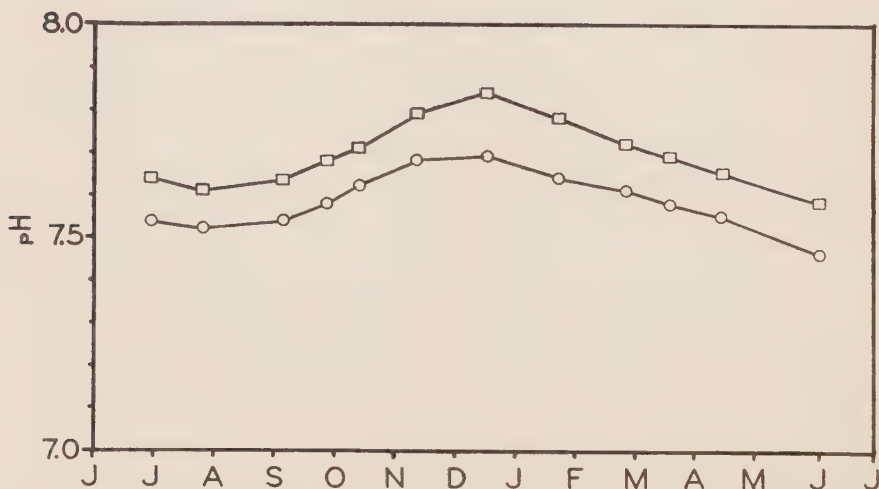


FIGURE 3. Seasonal variation at Station A of the pH of water at six meters depth (upper curve) and sediment (lower curve).

pH determinations at both stations agreed closely, and only the results at Station A are shown here.

In general, there was a slight increase in total phosphorus content in the water with depth. The concentration increased in the summer and decreased in the winter at all depths. The concentration of phosphorus in the sediment reached a maximum in midwinter and a minimum in summer. The increase of phosphorus in the sediment with decrease of phosphorus in the water, and vice versa, are illustrated in Figures 4 and 5.

DISCUSSION

Figures 4 and 5 show a decrease of phosphorus in the water with increase in the sediment. This suggests the possibility of a cyclic seasonal exchange of phosphorus between the sediment and water.

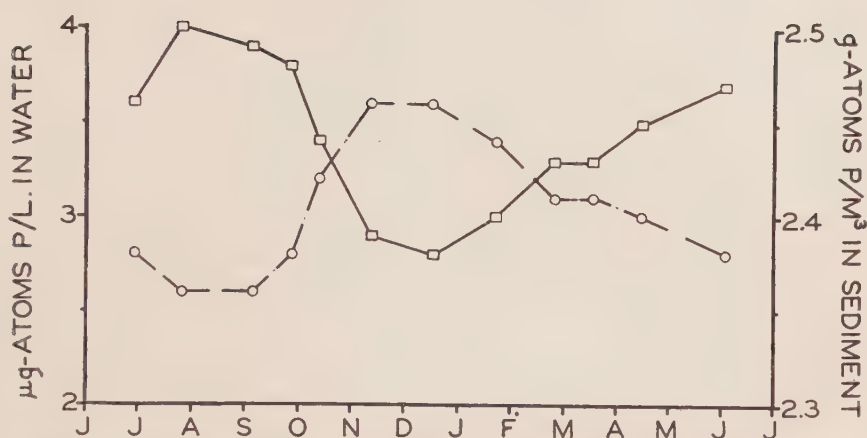


FIGURE 4. Seasonal variation at Station A of the phosphorus content of water (solid line) and sediment (broken line).

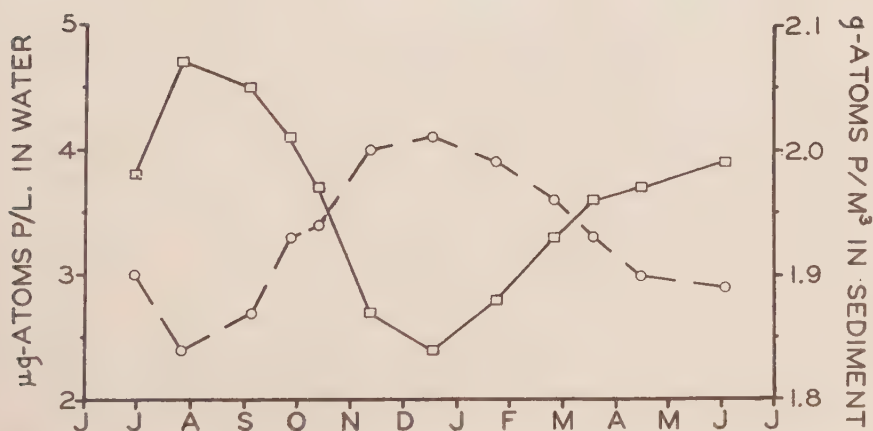


FIGURE 5. Seasonal variation at station B of the phosphorus content of water (solid line) and sediment (broken line).

The mechanism of the exchange in an analogous situation is explained in a report on the use of radioactive phosphorus as a tracer for lake nutrients by Hayes and Coffin (1951). In the spring the lake water is saturated with oxygen and there is a layer of oxidized mud at the mud-water interface, containing insoluble ferric phosphate. In the summer, the lower layers of water become depleted of oxygen and the ferric phosphate is reduced to the more soluble

ferrous phosphate. The ferrous and phosphate ions diffuse upward until they reach the thermocline, where the iron is oxidized to ferric iron by the higher concentration of oxygen, whereupon ferric phosphate is again precipitated. If hydrogen sulfide is present, the iron will precipitate as ferrous sulfide, and the phosphate will remain in solution, diffusing toward the surface of the lake.

During the present experiments, considerable quantities of iron in the sediment interfered with the separation procedure used in determining the total phosphorus content of the sediments by the accepted volumetric method. No particular significance was assigned to the incident at the time, but it now seems apparent that there was more than sufficient iron present in the sediment to have combined with all the available phosphate.

The variation in the pH of the sediment and of the water adjacent to it during the year enhances the possibility of similar mechanisms of phosphorus exchange in shallow marine basins and in fresh water lakes. In the spring and summer, the warm, relatively calm weather may result in anaerobic conditions in the sediment. This would cause the reduction of any ferric compound and form a crust on the surface of the sediment. The ferrous ion would dissolve, then immediately reprecipitate as the sulfide, and in this way release the anion formerly combined with iron and increase the hydrogen ion concentration. Comparison of the curves in Figure 3 with those in Figures 4 and 5 suggests a fairly close relationship between phosphorus exchange and pH of the sediment and overlying water.

The important phosphate deposits in the United States, including those in Florida and Tennessee, are primarily of marine origin. Although the original sedimentary source of these deposits was organic, the developmental processes were inorganic and physical. For a better understanding of the origin of these deposits it is desirable to have more knowledge of the diagenetic processes resulting in the concentration of phosphate as well as the environments where these processes are most effective. The concentration factor of sediment-phosphorus to water-phosphorus was found to be of the order of one thousand in the carbonate sediments at Hurricane Harbor (Figures 4 and 5). The concentration factor in other types of sediments and environments, and the distribution of phosphorus with depth in the sediment should be of assistance in locating regions where phosphate concentration processes are taking place.

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HEXAMITIASIS OF *OSTREA EDULIS* L. AND *CRASSOSTREA VIRGINICA* (GMELIN)¹

J. G. MACKIN², P. KORRINGA³, AND S. H. HOPKINS⁴

ABSTRACT

Ostrea edulis and *Crassostrea virginica* have been shown to contract a serious disease under conditions of low temperature, crowding, and recirculation of water in holding basins of Holland. This disease, known to the Dutch oystermen as "pit disease" is here designated as Hexamitiasis from the etiological agent, *Hexamita*. The flagellates are parasitic in the blood stream of their hosts, developing very heavy infections resulting in embolism and subsequent widespread histologic damage complicated by bacterial invasion and often resulting in death of the host. The disease occurs in America, as well as in Europe, and has been reported (unpublished mimeographed manuscript) from Prince Edward Island, Canada, and, in this paper, from Louisiana, where it is quite rare. Certain published data by Orton (1924) and Needler and Logie (1947) suggest that the disease may have caused extensive mortalities of oysters in the past.

INTRODUCTION

Studies on "pit disease" of oysters have led to such development of data on etiology and pathology that a preliminary report is desirable. "Pit disease" is a severe malady of *Ostrea edulis* in the basins or pits used by the Dutch oyster industry to hold oysters overwinter for convenience in marketing. The data indicate that the causative organism is a species of diplozoic flagellate belonging to the genus *Hexamita* Dujardin. Parasitization by *Hexamita* inflicts severe histologic damage on the host, and heavy losses from epizootics within the holding basins occur under certain conditions. There are indications that natural epizootics on planted beds may also occur. The disease has occurred in oysters at Prince Edward Island, Canada (Richardson, 1939), and also exists, but is comparatively rare, on the Gulf of Mexico coast of the United States.

HISTORICAL

The genus *Hexamita* was erected by Dujardin (1841) to contain

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three species of diplozoic flagellates (for extended taxonomic discussion see McNeil, Hinshaw and Kofoid, 1941). The type species is *H. nodulosa*, a form found in stagnant pools. Most species of the genus are parasitic and the hosts are insects, centipedes, amphibians, reptiles, fishes, birds and mammals. One species has been reported from oysters (Certes, 1882).

PATHOGENICITY

McNeil, Hinshaw, and Kofoid (1941) have summarized the data on pathogenicity of various species of *Hexamita*. According to these authors, the possible pathogenicity of *H. intestinalis* was first indicated by Moroff (1903). He recorded occasional heavy mortality of infected rainbow trout and observed a thinning of the intestinal wall at the site of infection but came to no definite conclusion regarding etiology. Ponselle (1919) recorded the death of a frog (*Rana*) presumably from heavy infection of the blood stream by *H. intestinalis*. The effect of the parasite was to produce an anemia. Lavier and Galliard (1925) found *Hexamita* in the blood of a toad (*Bufo*).

Schmidt (1920) regards *Hexamita* of trout as commensals, but states that he did not find the parasites in completely healthy fish. Moore (1923 a, b) found *Hexamita* to be the cause of pinhead disease of trout in American waters and in this was corroborated by Davis (1923, 1925). According to the latter author the disease is rare under natural conditions but becomes more common in hatchery ponds. He records development of lethal infections in young trout when transported under crowded conditions in metal containers. According to him the mortalities can be avoided by reducing numbers of fish in each container and limiting the transportation period to less than 24 hours.

Pathologic effects of infection of the bladder of tortoises by *Hexamita* were described by Grasse (1904) who thought that the parasites might penetrate the tissues.

A disease of pigeons was described by Noller and Buttgerit (1923). The small intestine contained *Hexamita* and the effect was a catarrhal enteritis of considerable severity. Hinshaw, McNeil and Kofoid (1938a, b) described a similar disease of young turkeys which caused heavy mortality. They later (McNeil, Hinshaw and Kofoid, 1941) further discussed this disease which they definitely ascribed to *Hexamita meleagridis*, gave additional structural details

of the parasite, and reviewed the literature on pathogenesis of flagellates of the genus.

Several other species have been described from various hosts, but no pathogenic role has been ascribed to any excepting those mentioned. *Hexamita* of the wood roach is reported to be symbiotic. Thus the genus is represented by free living, symbiotic, and parasitic species. The effects of parasitism range in severity from production of a mild enteritis to lethal disease.

HISTORY OF *Hexamita* IN OYSTERS

Certes (1882) recorded *Hexamita inflata* from the stomach of oysters (*Ostrea edulis*), which is apparently the earliest record. So far as the authors are aware, this is also the only published record. However, there is at least one unpublished record (Richardson, mimeographed report, 1939) and another published record of flagellates (under the name of *Bodo*) which were probably *Hexamita*. This latter record was by Orton (1924).

In this case Orton was studying possible causes of the famous mortalities of English oysters occurring in 1920-21. He encountered flagellates in the pericardial fluid of weak and gaping oysters which he supposed to be a species of *Bodo*, probably a misidentification, since members of this genus are free living or coprozoic. Orton concluded that because he could not produce infection by feeding cultures of the flagellates to oysters that they were "saprophytic"; *i. e.*, invaders after or near death of their hosts. However, his description of the diseased oysters shows many points of similarity to Hexamitiasis, and especially his drawings of "inclusion" bodies which are quite close reproductions of intracellular stages of *Hexamita*. Orton's paper is of such interest that it will be discussed in more detail in a later section.

Richardson in 1939 studied certain phases of mortalities of oysters of Prince Edward Island, in Canada. He found *Hexamita* in oysters and included his findings in a mimeographed report which was made available to the authors through the kind cooperation of Dr. R. R. Logie. Richardson was fully aware of the pathogenicity of the *Hexamita* of oysters (*Crassostrea virginica*) and gave details in a conversation with the senior author. He stated (1) that the flagellates penetrated oyster tissues and were so observed by him in diseased oysters, (2) that it was his opinion that the disease was highly lethal and that the mortalities of Malpeque Bay oysters described by Needler

and Logie (1947) were largely caused by *Hexamita*. Dr. Richardson therefore was the first to observe the flagellates in American oysters and the first to ascribe to them a pathogenic role in oyster disease.

HEXAMITIASIS OF *Ostrea edulis* AND *Crassostrea virginica*

The present studies were initiated because it was apparent that some mortality agency additional to shell disease was acting on *Ostrea edulis* in Dutch waters and especially in holding basins. These basins are for storage of marketable oysters and primarily for facilitation of sale during winter months. Water in the basins is exchanged daily. In some newly constructed, temperature controlled basins the water can be recirculated during cold spells. A pumping system maintains a circulation in these basins. Some new water is added daily. Temperature is controlled at 3° to 5° C. Checks on salinity during the winter seasons of 1950 and 1951 showed that it varied but little from about 28‰. Oxygen was 90 to 98 per cent saturation and organic matter was normal. Major environmental factors were therefore approximately normal for *O. edulis* in the temperature controlled basins, of which one had been operated for several years without mortality to speak of. The oystermen know, however, that in the normal open basins, in which the water is changed daily, some oysters may die for no obvious reason during storage, especially in the early spring. This mortality, called "putziekte" or pit disease by them, was not of a serious nature in recent years, but has been more severe in the past. During the early months of 1950, however, a considerable mortality was observed in two temperature controlled basins at Yerseke in which the water was recirculated. Transfer of oysters from affected basins to other basins or to plots failed to stop the mortality. Oysters generally died fat and from external appearances seemed to be in excellent condition. All the weak (hockley) and dying oysters appeared to have a very light, fauny color of the digestive gland instead of the chocolate-brown of the digestive gland of a healthy oyster. Later in the year mortality stopped in these basins. During 1950 no abnormal mortality occurred at Bergen op Zoom, although basins there also used recirculated water.

Early in 1951 pit disease reappeared, this time in basins at Bergen op Zoom. Early in March cluckers, and then many gapers, appeared. These oysters also were fat and with good glycogen content. Mortalities also occurred at this time in a basin with recirculated water at Wemeldinge. Some unusual mortalities, accompanied

by a very light coloration of the oyster's digestive gland, also occurred on planted beds on the Yersche Bank. Mortalities continued into April, but in May the wave of losses had subsided.

Dutch fisheries inspectors point out that most mortalities in Holland occur in early spring and not in high temperature summer months. The mortality on the beds in the spring of 1951 was the first appearance of any considerable losses of this kind for a great number of years, and coincided with rather high population of planted oysters. It has previously been shown (Korringa, 1947) that heavy losses in the past coincided with unusually dense plantings.

INCIDENCE OF HEXAMITIASIS

The present study is based on a considerable number of specimens of live *Ostrea edulis* and a smaller number of gapers from beds and holding basins in Holland. These oysters were fixed in Bouin's fluid (an unsatisfactory fixative) and Zenker's fluid, sectioned at seven microns and stained with Heidenhain's iron haematoxylin and eosin, with Delafield's haematoxylin and eosin, and with Giemsa. In all 76 oysters (*Ostrea edulis*) were sectioned and studied for disease and presence of *Hexamita*. Of these 16 were cluckers but all were still alive. Of the 16, nine were infected by *Hexamita* in the trophozoite stage. All nine of these were taken from storage basins. Of the 60 apparently healthy oysters, four had *Hexamita* in the trophozoite stage and these also came from storage basins. No oysters from planted beds were infected by *Hexamita* in the trophozoite stage, although several oysters had intracellular stages looking very much like the intracellular stages found in undoubted cases of *Hexamita* identified by the presence of trophozoites. It is apparent from these figures that *Hexamita* infection is enhanced by the conditions in the holding basins. These conditions probably are (1) near optimum temperature, (2) crowding in trays, and (3) recirculation of the water. It is also evident that attainment of crowded conditions and low temperature on planted beds might well precipitate an epizootic.

Out of about 2000 oysters sectioned and studied for disease in southern Louisiana, about a half dozen cases of Hexamitiasis have been observed. These were all in gapers. It is apparent that incidence in the Gulf area is quite low, probably because temperatures are not optimum. All cases were observed in winter or early spring months, but temperatures at time of observation were between 15° and 20° C. This apparently marks a near maximum temperature at

which the parasites develop and indicates a quite wide range of adaptability in this respect.

STRUCTURE OF *Hexamita* OF OYSTERS

Figure 1 is a semi-diagrammatic representation of the trophozoite of

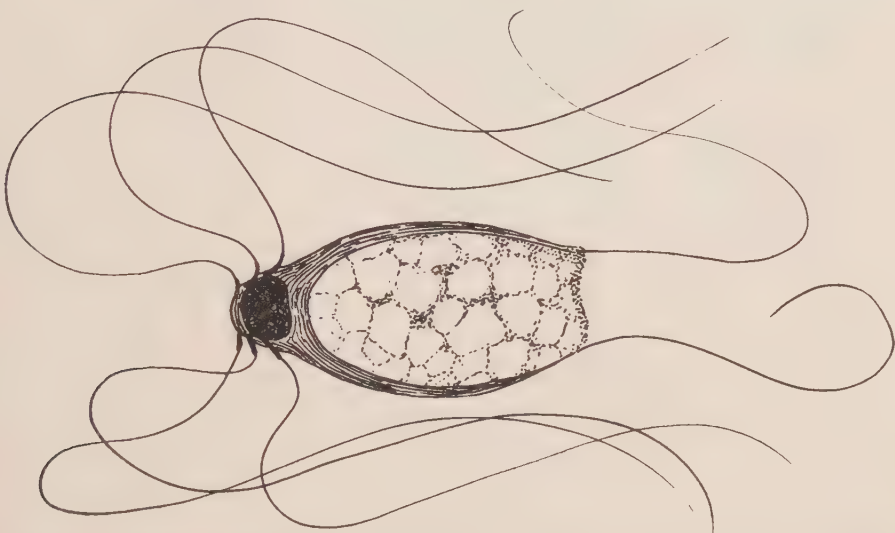


FIGURE 1. Semi-diagrammatic sketch of a trophozoite of *Hexamita* showing flagella and axostyles.

Hexamita sp. found in oysters. The nuclei are placed very far toward the anterior end and are so tightly appressed that they appear as one. They seem to be contained within a skeletal structure made up of the basal portions of the very thick axostyles. These latter are very widely separated, lying against the pellicle, and stain deeply with haematoxylin. General body shape is an oblong oval narrowing anteriorly. There are the usual six anterior flagella each set on a thickened basal portion, and two posterior trailing flagella. Internally the stained trophozoites either appear to be empty or have a light granular and reticular cytoplasmic structure. Living trophozoites have not as yet been studied although a few have been observed.

In advanced stages of disease connective tissues and blood channels of the host contain cysts of the flagellates. These are thin walled, with two or four small deeply staining nuclei and no flagellar structures

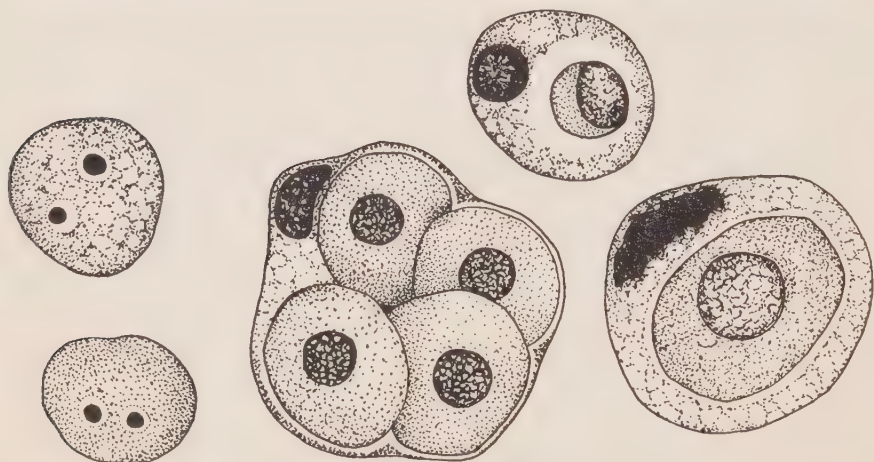


FIGURE 2. Binucleate cysts and intracellular cells of *Hexamita* from sections of an infected oyster. The cysts are about 5 microns in diameter.

(Figure 2). Disintegration of the host would be necessary to liberate these into the water.

Of very considerable interest are the intracellular stages found in leucocytes of the blood vessels. These are most abundant in relatively early stages of development of disease and precede the appearance of large numbers of trophozoites. Characteristically there is one cell to each host cell, but there may be as many as four or five. Hypertrophy of the host cell results from invasion, and when several are in a single host cell, very large round leucocytes result. The appearance in sections of large numbers of odd sized leucocytes aggregated around the basal membrane of the digestive tube is almost certainly diagnostic of *Hexamitiasis*, especially if fibrosis is absent. An intracellular cell of *Hexamita* has a centrally located large rounded nucleus, which differs but little from that of the host cell. In many instances the included cell lies in a vacuole of the host cell. Some very small inclusions may possibly be early invading infective elements but this is probably not true. An effort has been made to piece the various intracellular elements of the intestinal epithelium and the leucocytes into a cohesive life cycle without success. Considerably more refined methods of fixation and staining will be necessary before the significance of the intracellular stages of *Hexamita* of oysters is understood. It may be that the intracellular cells are leucocytes, ingested by other leucocytes under stimulation of parasitization. The early appearance of the intracellular

stages preceding that of trophozoites would seem to negative this interpretation.

HISTOPATHOLOGY OF INFECTION

Early stages of disease observed in *O. edulis* show that the site of infection is the blood, parasites being found in arteries and sinuses throughout the body. There is no indication of what the portal of entry may be. Trophozoites have been found but rarely in the intestinal and stomach lumina. It is probable that infection is by means of cysts, since early stages of disease show but few trophozoites and a preponderance of peculiar intracellular stages in leucocytic cells (Figure 2). The outstanding histologic picture is of blood vessels packed tightly with leucocytic cells. It is the only disease of oysters so far observed in which leucocytes remain in the blood channels rather than aggregating in connective tissues, and this emphasizes the fact that the normal medium of the parasites is the blood.

Early in the course of infection the leucocytes show signs of degeneration and necrosis. Hypertrophy is common, whether the leucocytes bear intracellular stages or not. Cytoplasmic degeneration is indicated by the accumulation of deep staining granules, vacuolization, and a tendency to change to a basophilic reaction. The nucleus may become irregular or pycnotic and often is appressed against the cell wall, even when no visible inclusions are present in the cytoplasm. Late stages show a very great loss of leucocytes, indicating an impairment of productive capacity.

There is a tendency for leucocytes and intracellular parasites to aggregate in sinuses in the region of the basal membrane of the stomach and intestine, producing a characteristic inflammation. To a lesser extent this inflammation extends throughout the visceral region especially in the digestive gland. When the accumulation has reached the point of saturation so far as blood sinus space is concerned, breakdown of connective tissue cells occurs, which breakdown spreads throughout the body. The appearance of heavy concentrations of trophozoites in blood vessels (Figure 3) is followed by widespread destruction and necrosis of nearby tissues. Trophozoites apparently are to some extent localized, since abscesses are sometimes encountered in which nothing remains but tissue debris and trophozoites, while other areas of the same slide may be relatively free of intense infection.

Secondary effects of parasitization are to be observed in the gonads. In all cases of the disease encountered, eggs are obviously in a state

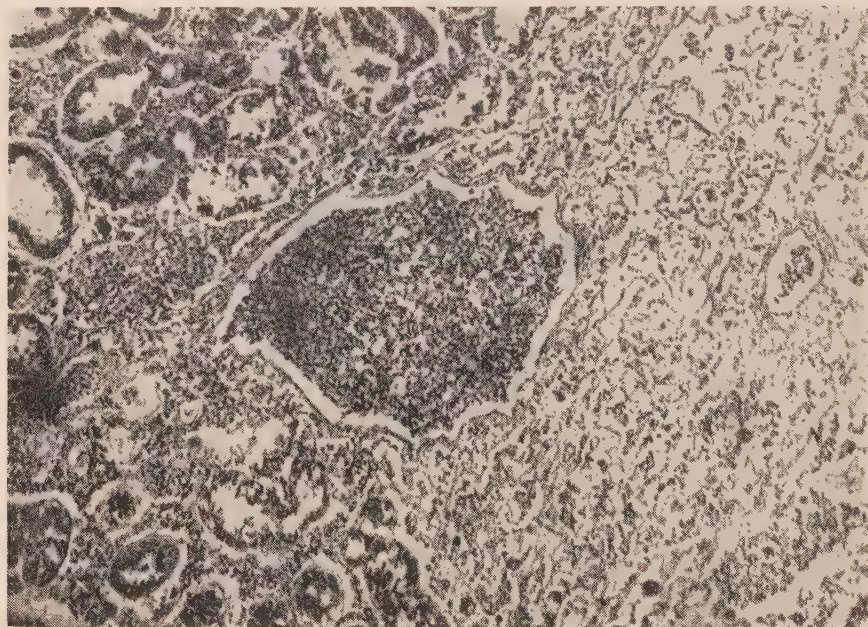


FIGURE 3. Photomicrograph of a mass of trophozoites of *Hexamita* blocking a blood vessel and penetrating surrounding tissues in the edge of the digestive gland. Magnification about 100 X.

of degeneration, tending to liquefy or develop inclusion bodies. Since this same phenomenon has been observed in oysters in which infection by *Hexamita* has not been demonstrated, the relation of the parasites is rather uncertain.

The epithelium of the digestive system undergoes degenerative changes both in the stomach and intestine and in the ducts of the digestive gland. Small spheres, looking much like intracellular cells, accumulate in the basal part of the epithelium. These may be intracellular stages of *Hexamita*, since they resemble very much certain stages figured by Davis (1925) in the intestinal epithelium of trout parasitized by *Hexamita salmonis*. However, it is thought best to merely record these cell-like bodies at present, and leave their significance to future studies. Irrespective of their nature, they accumulate at the expense of the epithelial cells which are often completely destroyed over wide areas. Accumulation of granular deposits takes place throughout all epithelia and is interpreted as indicating necrosis.

The muscle spindles described by Orton (1924) appear in all

tissues and blood channels, indicating muscular breakdown. Two cases of *Hexamita* in the adductor muscle have been observed. Muscles of the mantle also are broken down. The appearance of myolytic spindles in the blood of oysters, or in the tissues in sections is probably the best of all indicators of severe disease.

All heavy infections in *Ostrea edulis* have been accompanied by massive bacterial invasion. This probably results from withdrawal of leucocytes into the blood channels and away from the digestive tract. Bacilli of several types have been observed in the intestinal lumen and the ducts and tubules of the digestive gland. Here they may occlude the lumen and invade the epithelium. The intestine and tubules always contain considerable tissue debris in heavy infections and the bacteria multiply in these masses. In some cases they occurred in large numbers in the blood and connective tissues as well as in the digestive tract. It is assumed that these bacteria are secondary invaders for the following reasons. First, oysters lightly infected by *Hexamita* do not have the bacteria, showing that bacterial infection follows that by *Hexamita*. Second, the type of bacterium varies with different oysters, although one spore-bearing bacillus occurs in most of them. Third, in *Crassostrea virginica* there are no bacterial invaders so far as can be determined from study of sections, even in heavy infections (the only kind of infection positively identified in this host).

At this point it may be well to mention that normal food elements have not been seen in the digestive tract of any oysters with trophozoites in the blood stream. The significance of this is not clear since some apparently normal oysters from basins also were without food.

DISCUSSION

The data indicate a highly lethal disease caused by *Hexamita*. The development of epizootics appears to rest on circumstances which favor transmission of infective elements from host to host, namely crowded conditions and a circulating medium. These conditions are realized in some lately constructed Dutch basins where the water is recirculated. Mortality did, however, also occur in earlier years in open basins crowded with oysters. It seems that the water temperature held at 3° to 5° C. is near optimum, but it may be that a higher temperature is optimum and that the crowded conditions and recirculation of the water produce epizootics at a temperature below optimum, because of reduced resistance of the host.

It has been a matter of great interest to the authors that Orton

(1924) described in great detail what seems to be the Hexamitiasis disease observed by us. The points of coincidence are several. Included would be (1) production of myolytic spindles which are found in blood and tissues of the host, (2) concentration of leucocytes in large number in vessels and sinuses of the blood system, (3) concentration of leucocytes around the basal membrane of the digestive tract, (4) necrosis of epithelium of the digestive tract, (5) development of abscess filled with tissue debris, (6) ovarian degeneration and liquefaction of eggs, (7) development of secondary saprophytic bacterial infections, (8) intracellular elements in leucocytes, (9) tendency of hockley oysters to die fat, and (10) a light, tawny yellowish color of the liver. None of these is specific for Hexamitiasis, but when all are taken together, they are at least suggestive that the English oyster mortalities of 1920-21 may have been due to this disease.

It is interesting also to examine the data as regards Hexamitiasis and the Prince Edward Island mortalities as reported by Needler and Logie (1947). The facts here are meager but none the less suggestive. Richardson found Hexamitiasis in Malpeque Bay oysters in the same situations in the host as reported in this paper. There seems to be little doubt that the parasites were abundant when he studied them in 1939. There also can be little doubt that *Hexamita* under optimum conditions can produce epizootics with heavy mortality. There is therefore the possibility that the etiological agency in the case of the Prince Edward Island mortality waves was *Hexamita*, which opens the further possibility that other low temperature areas (as Long Island Sound) may harbor the disease as an endemic condition. There is a compensating factor also. The data presented by Needler and Logie (1947) strongly suggest that oysters develop an immunity to infection, and that, in an endemic area, only non-immune imports are likely to take heavy losses.

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PHYSICAL FACTORS AFFECTING THE DISTRIBUTION OF EUPHAUSIDS IN THE NORTH ATLANTIC¹

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ABSTRACT

A theoretical relationship has been developed between the environmental temperature and the survival index of a planktonic organism. The significant temperatures are the degree of departure from the optimum values of surface temperature (T_s) and temperature at the depth of 10^{-12} illumination (T_{I-12}). Allowance is included for cases where the optimum is closer to the upper than to the lower limit of tolerance, and also for a degree of physiological adaptation. It is considered that the survival index of a species in a given habitat should be reflected approximately in the relative abundance in that habitat of the species in question among the total population.

The geographical distribution of Euphausiids in a considerable part of the North Atlantic and Mediterranean is charted. Charts are also given, for the same area, of the distribution of the extinction coefficients of the water and of the calculated values of T_{I-12} . The relation of the abundance of each of the commoner species to T_s and T_{I-12} is given.

A good agreement is found between theoretical and observed temperature relationships if it is assumed that, for most species, there are two different temperature optima, one associated with the day level and the other with the night level. The likelihood of such a dual temperature control is discussed.

For a few species, critical temperatures as indicated by scattering layer records are compared with those indicated from geographic distribution. Finally, for *Euphausia hemigibba*, the geographic distribution, as predicted from physical conditions, is shown to agree reasonably well with actual observations.

INTRODUCTION

In a previous paper (Moore, 1950) it was shown that the diurnal migration of Euphausiids is primarily influenced by illumination, with temperature as a modifying influence during part of the cycle. In an area such as the Mediterranean, where there is little thermal stratification of the water, their movements as deduced from the records of the scattering layer, tend to maintain them throughout the daylight hours at a constant illumination. In the stronger thermal stratification of the Atlantic, their morning descent carries them down through a greater temperature range. Correlated with this condition, their de-

¹ Contribution No. 581 from Woods Hole Oceanographic Institution.

Contribution No. 68 from The Marine Laboratory, University of Miami.

scent follows the changing illumination for its first period, but beyond a certain depth, descent ceases, despite the now increasing illumination. This level is maintained throughout the midday period until a time in the afternoon when the decreasing illumination takes control again, and the evening ascent is commenced. That temperature is the factor concerned is indicated by the dependence of the depth at which this "noon flattening" of the migration curves occurs on local temperature distribution.

It was postulated that the temperatures encountered at the vertical extremes of the diurnal migration were limiting factors in the geographical distribution of a species, and it was shown that the distribution of these two temperatures was adequate to explain the distribution of the commoner Euphausid species in the western North Atlantic. In the present paper, the effects of temperature are considered in greater detail, and the theoretical relationship arrived at is compared with observed Euphausid distributions. For the latter, a very much wider area of the North Atlantic has now been covered.

The author gratefully acknowledges the assistance, both with advice and in obtaining material and data, of the staff of Woods Hole Oceanographic Institution and the Marine Laboratory, University of Miami. In particular, Mrs. Andrew Bunker has carried out a large part of the abstracting and calculating as well as examining many of the plankton samples.

THEORETICAL CONSIDERATION OF TEMPERATURE EFFECTS

During the course of its diurnal migration cycle, an animal inhabits two widely different environments. Not only may these differ by as much as 10 or more degrees in temperature, but they differ also in phytoplankton content, oxygen concentration and other factors. The night environment is near the surface where the phytoplankton supply is rich. Too low a temperature here might be expected to result in decreased activity and lowered feeding rate. The same might be true of too high a temperature, and if the Euphausids avoided this by remaining at deeper and therefore cooler levels, their food supply would be less. Thus an optimum temperature may be assumed to exist for the night conditions. At the deeper day level the feeding rate is presumably much less. If at that level the temperature is too low, then the animal can only avoid it by enduring the greater illumination associated with higher levels. On the other hand, if the temperature is too high, then an impossibly extensive vertical migration may be

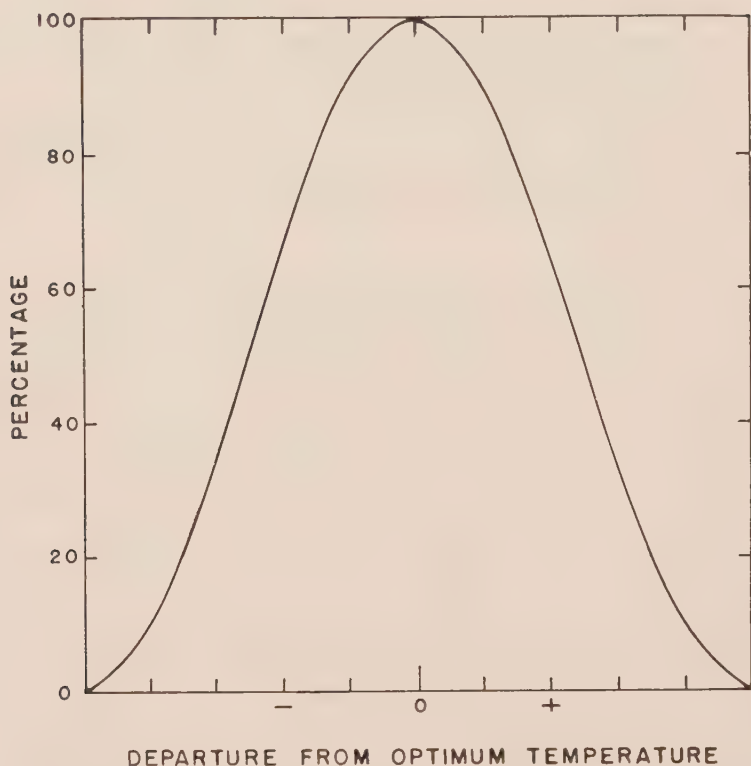


FIGURE 1. Hypothetical curve relating survival index to departure from optimum temperature. No temperature units are shown since these vary in different cases.

involved if sufficiently low temperatures are to be reached. Thus an optimum day temperature also is postulated.

The ability of an organism to survive, and the success with which it does this, is a highly complex process, dependent on various external and internal conditions. Fischer-Piette (1948) has discussed this, and has shown that the "prosperity" of the organism may be measured in many ways. The optimum environmental conditions vary considerably according to the aspect of this prosperity which is considered. In a later section of the present paper, the prosperity of the various Euphausiid species will be assessed in terms of their abundance relative to one-another. Although this involves inter-specific competition, it is assumed that their ability to compete depends on the degree of suitability of other environmental conditions. Since the processes in-

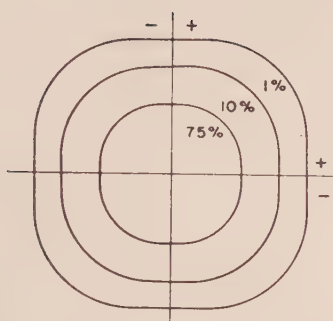


FIGURE 2.

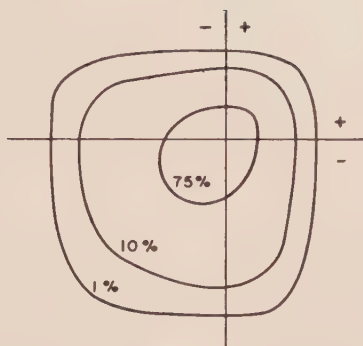


FIGURE 3.

FIGURE 2. Relation of survival index to departure from optimum temperature in a case involving alternation between two climates, in both of which there is a symmetrical response above and below the optimum.

FIGURE 3. As in Figure 2, but with an asymmetrical temperature response in which the lethal limit is further below than above the optimum.

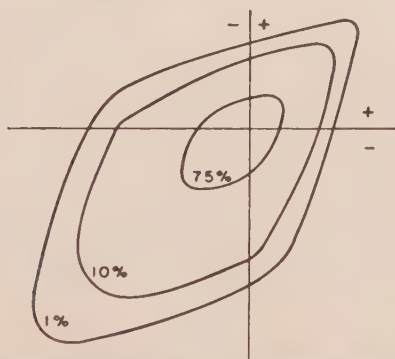


FIGURE 4. As in Figure 3, but involving physiological adaptation also.

involved are so little understood, the deliberately vague term "survival index" is used here. In considering the effects of temperature, this index is given a value of 100 per cent when optimum temperature conditions are present, and 0 per cent when conditions are beyond the tolerance range of the species.

Since considerable simplification of the problem is necessary, let us assume that there is a simple relationship between this survival index and temperature, and that this follows the limited section of a sine curve shown in Figure 1. Actual values are omitted from the temperature scale, since they will vary from one species to another and there is no implication that there is an actual sine relationship. Since two

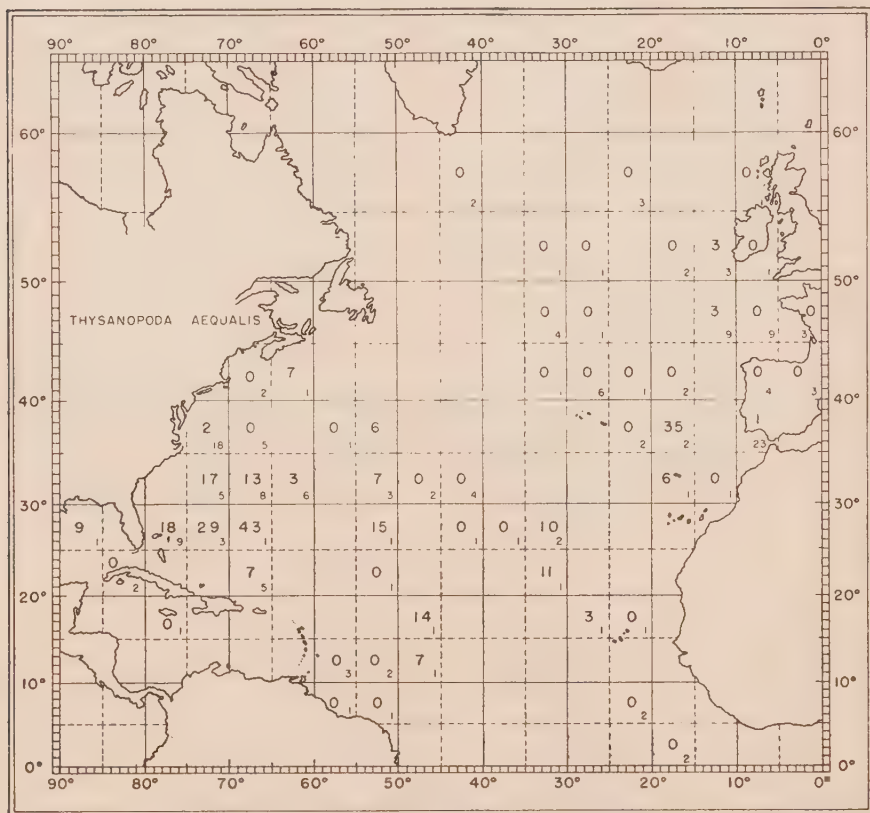


FIGURE 5.

FIGURES 5-14. Geographic distribution of Euphausiids expressed as the percentage of each species in the total Euphausiid population (excluding the genus *Stylocheiron*). Values are averages for 5° squares, and the suffixes in Figure 5 show the number of samples available for analysis in each square.

different environments are involved in the diurnal migration cycle, the survival index for a species in a given locality will be a function of the degree of departure of both the day and the night level temperatures from the optimum temperature. For simplicity, it may be assumed that the overall survival index of the species for that locality is the product of the indices for day and night conditions, both of these being read from the curve given in Figure 1. Figure 2, therefore, represents the overall survival index for all possible relations of the day and night temperatures to the optimum temperature. Part of this

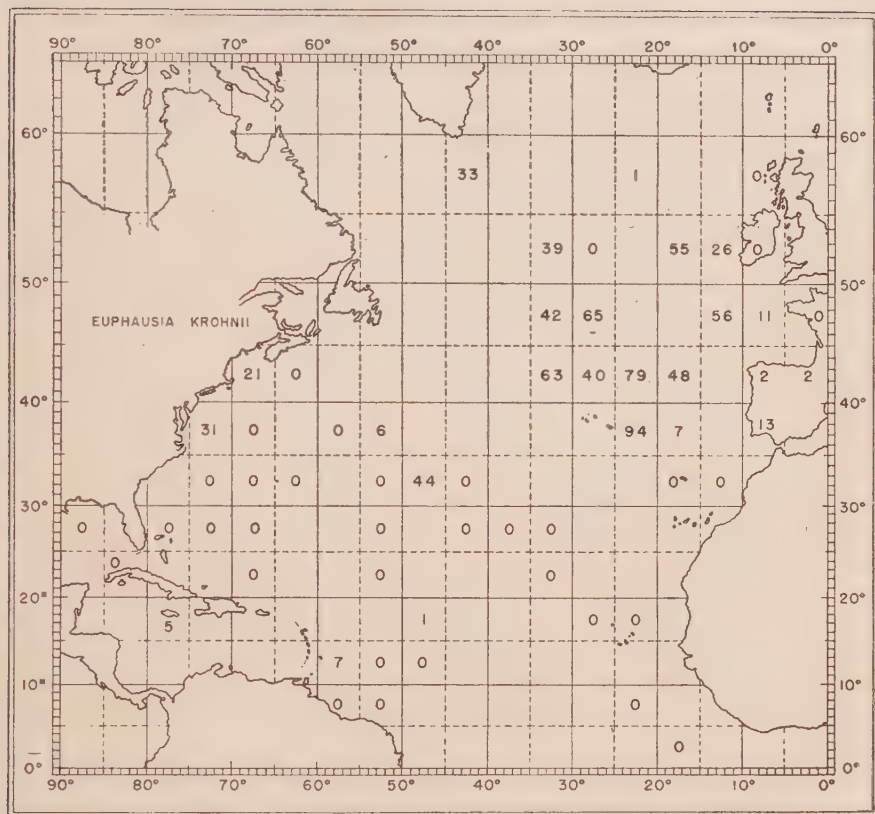


FIGURE 6.

array represents conditions which would be unlikely to be encountered under natural conditions, since the surface temperatures would have to be lower than the deep ones. This could occur only where the effect on density was compensated for by corresponding salinity differences.

For many organisms, the lower lethal temperature is further from the optimum than is the upper limit. It would therefore be better to modify the curve in Figure 1 to give a more extended scale on the left of the optimum. If this is done, a pattern of the type shown in Figure 3 is obtained for the relationship of survival index to two varying temperatures. A still further modification is called for to allow for the physiological adaptation which frequently occurs and may result in physiological races. This may be represented here by a shift of the optimum in Figure 1, the amount of the shift being a function

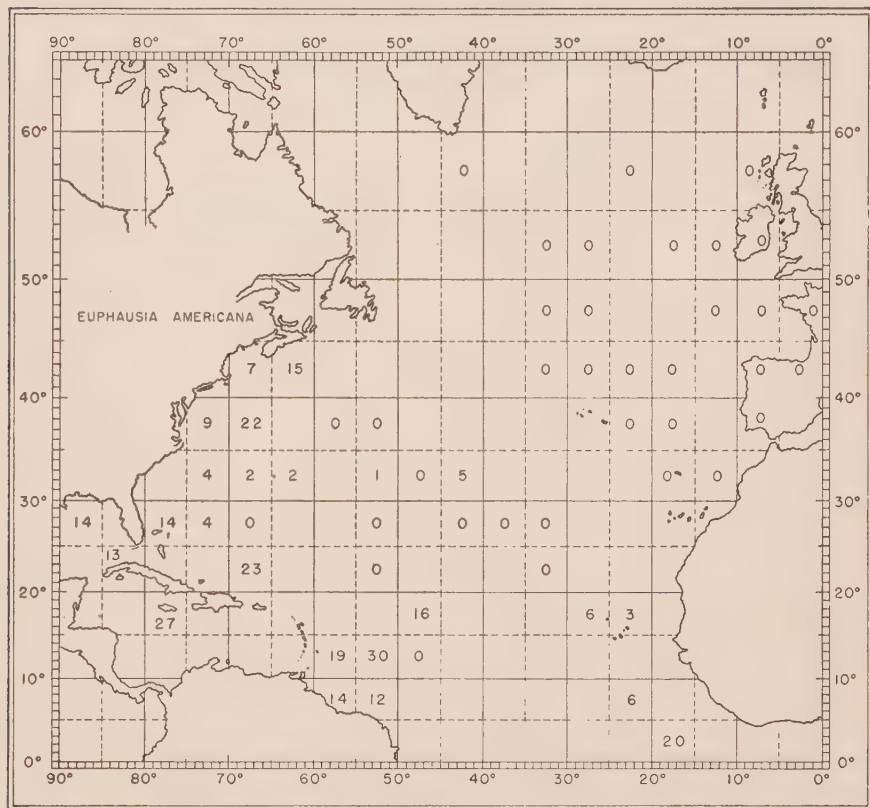


FIGURE 7.

of the average departure of the environment from optimum conditions. If an initial optimum value is assumed, then the adapted optimum may be considered as having shifted by half the mean of the departures of the day and night temperatures from the initial optimum. While based on arbitrary assumptions, this yields the required effect of a higher degree of physiological adaptation where both temperatures depart in the same direction from the initial optimum, and sets a limit to the extent of physiological adaptation possible. With maximum physiological adaptation, the survival index is 0 per cent when either of the two temperatures departs from the optimum by twice the maximum permissible unadapted departure. When such allowance for physiological adaptation is made, curves given in Figure 3 are modified to give the more elongate pattern shown in Figure 4.

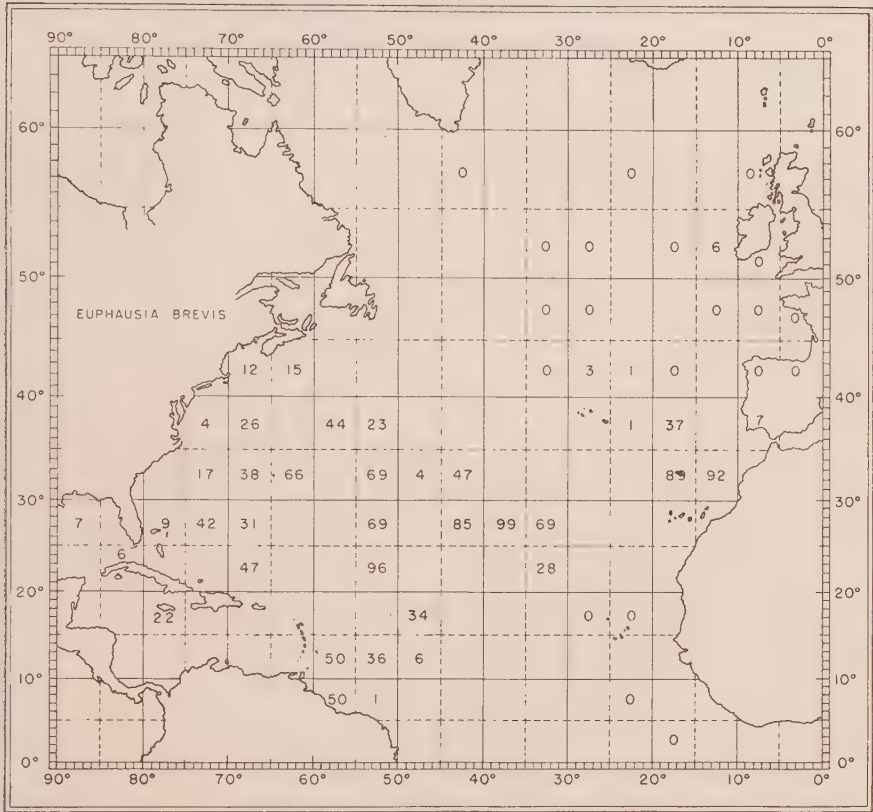


FIGURE 8.

OBSERVED GEOGRAPHICAL DISTRIBUTION OF EUPHAUSIDS

Data on geographical distribution have been taken from all available published sources, together with samples taken by R. V. "Atlantis" and other vessels. Only those sources which provide numerical information on relative abundance have been included, and data from areas from which the necessary hydrographic data are lacking have been omitted. Unfortunately, the absence of information on transparency for the area has required the omission of much of the data given by Einarsson (1945). The same is true of the stations in the northern part of the Mediterranean, given by Ruud (1936). As in earlier work, the abundance of a species has been expressed as its percentage in the total Euphausiid population at that place, but the

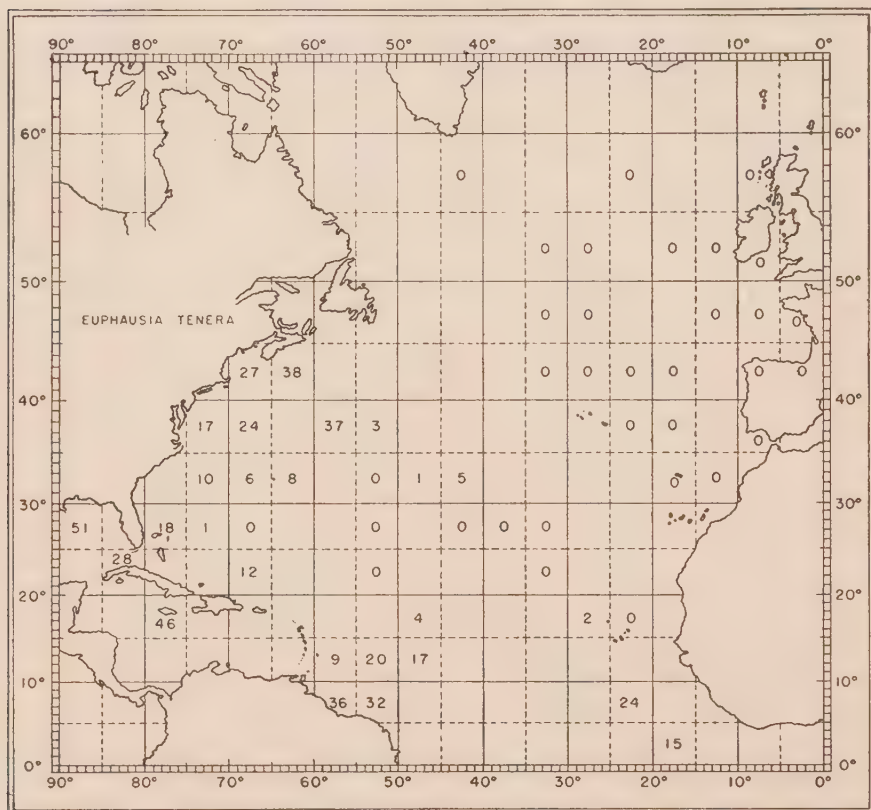


FIGURE 9.

genus *Stylocheiron* has been omitted in the calculation of the latter. Various types of net hauls are included, and all are not of the same significance. Where a series was taken at a single station, their combined content has been treated as a single haul, but samples below about 500 fathoms have not been included. The fact that many of the "Atlantis" hauls were made at the surface at night, together with the reversed type of diurnal migration found in some species of *Stylocheiron*, justified the omission of that genus. The results for 10 of the most common species of the area are shown, averaged by 5° squares, in Figures 5-14. Since we are mainly concerned with the warm water species of the Atlantic, only one northern form, *Thysanoessa longicaudata*, has been included for comparison. In part of the area under consideration, such forms as *Meganctiphanes norvegica*

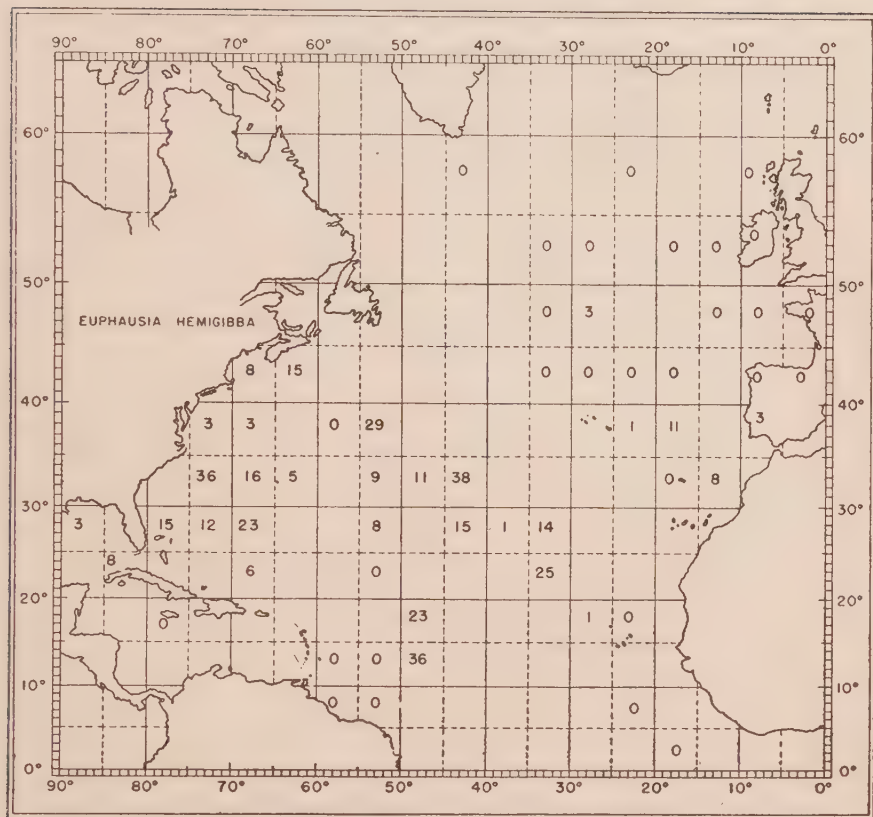


FIGURE 10.

are abundant. These have been omitted because they are northern forms, and, in this case, because their ability to live in shallower water than the typically oceanic species, complicates the picture. Dr. M. V. Lebour (*in litt.*) has suggested that the present *Thysanopoda aequalis* requires revision, and may prove to be composed of more than one species. Our results do not show any marked discontinuity of distribution or other characteristics, but such would not of necessity be expected. *Euphausia americana* and *E. krohnii* were, at one time, confused, but were adequately separated throughout the records utilized here. *Nematoscelis microps* has been included, but is subject to doubt as to the validity of some of the identifications.

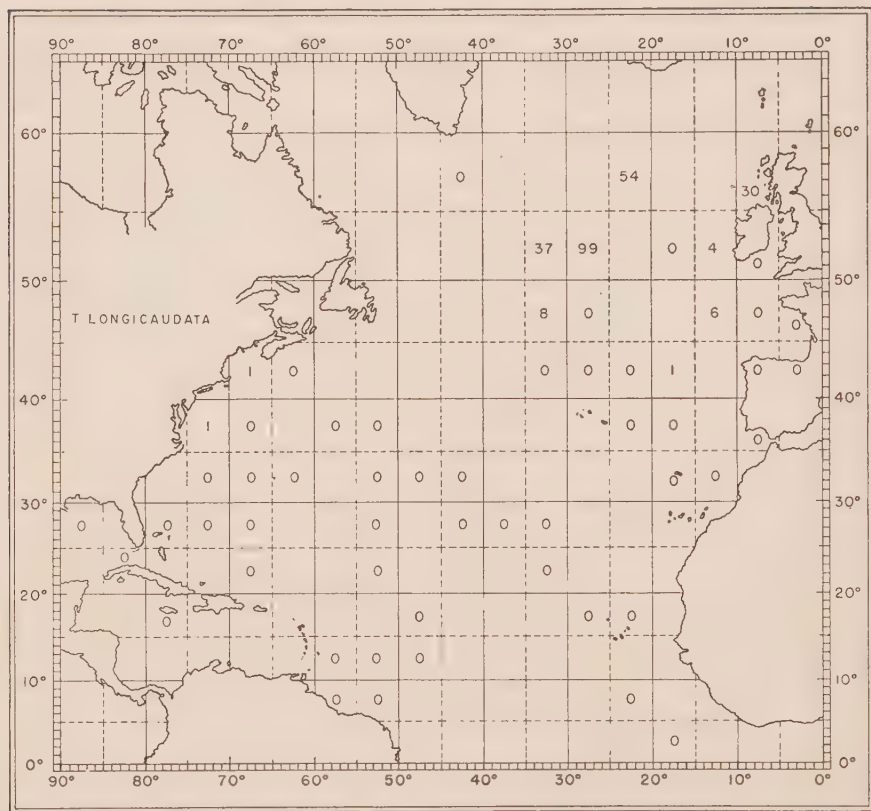


FIGURE 11.

TEMPERATURE DATA

The best night level temperatures to use would no doubt be the average or extreme value for the year at the depth occupied by each species at the locality in question. Lacking adequate information on the night levels occupied, we have had to make use of surface temperatures instead. Further, since maximum summer surface temperatures were used in previous work, this value has been retained here. While these cannot be taken as identical with the temperatures actually encountered by the animals, they may be assumed to be correlated with them but strictly they represent only certain surface characteristics of the water in which each species lives. Since hydrographic data were not always collected along with the net hauls, use has been

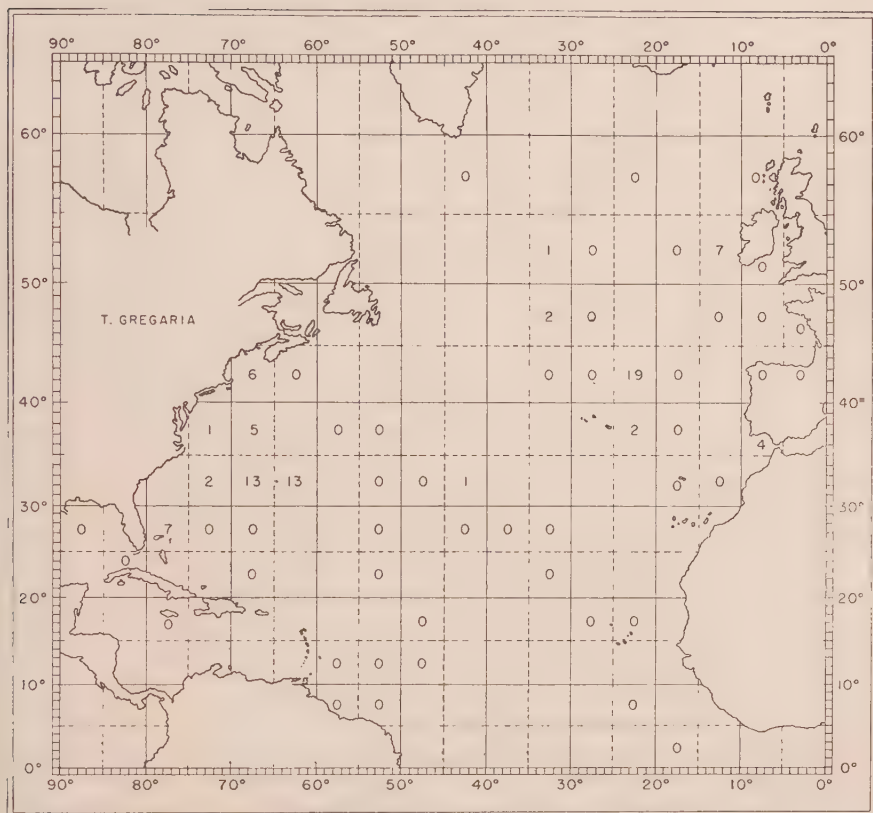


FIGURE 12.

made of charts of summer temperatures based on information in the hydrographic files of Woods Hole Oceanographic Institution. An error, due to the net hauls and the hydrographic observations not being simultaneous, is therefore introduced, but this is considered to be relatively unimportant.

Since, at the day level, both temperature and illumination are controlling factors, a combined factor was introduced in previous work. This was the illumination at the depth of 16°C. isotherm. In the present survey we are concerned primarily with temperature. In addition, areas are included where the temperature, even at the surface, is not as high as 16°. A more satisfactory factor to define deep conditions has therefore been found in the temperature at the depth at which the illumination at noon in summer has a value of 10⁻¹² (re-

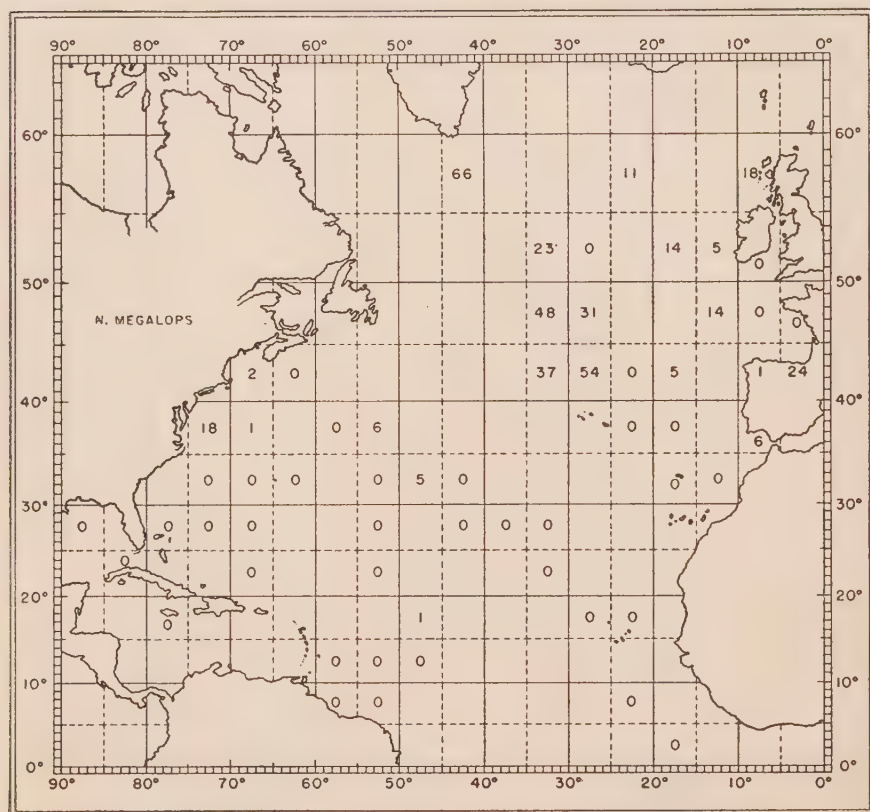


FIGURE 13.

ferred to hereafter as T_{I-12}). This is of more widespread application, but yields a very similar distribution pattern to $I_{T=16}$ for the area of the western North Atlantic included in earlier work. As in the case of the night level temperature (T_s), this does not represent the actual day temperatures encountered by the Euphausiids, but their variation from one area to another may be taken to be sufficiently closely correlated to allow certain comparisons to be made.

For the estimation of T_{I-12} , it is necessary to know the transparency of the water. Figures 15 and 16 show the distribution of extinction coefficients for the North Atlantic and Mediterranean areas. These are based on published information together with observations made by R. V. "Atlantis," U.S.C.G. Cutter "Evergreen" and other vessels, all of which are available in the hydrographic files already referred

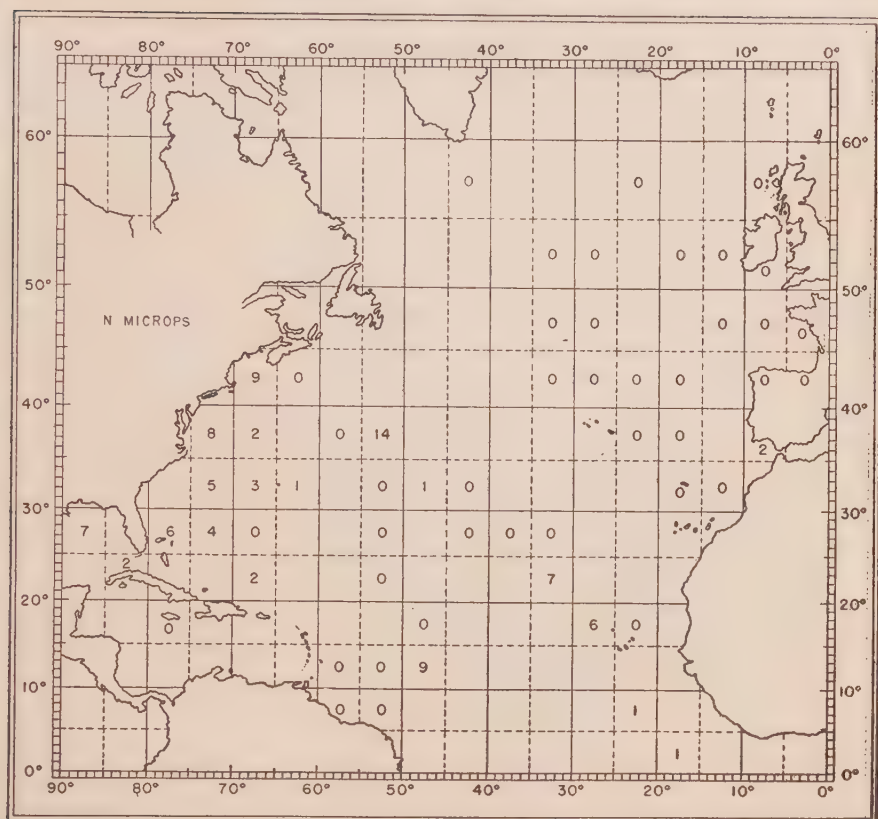
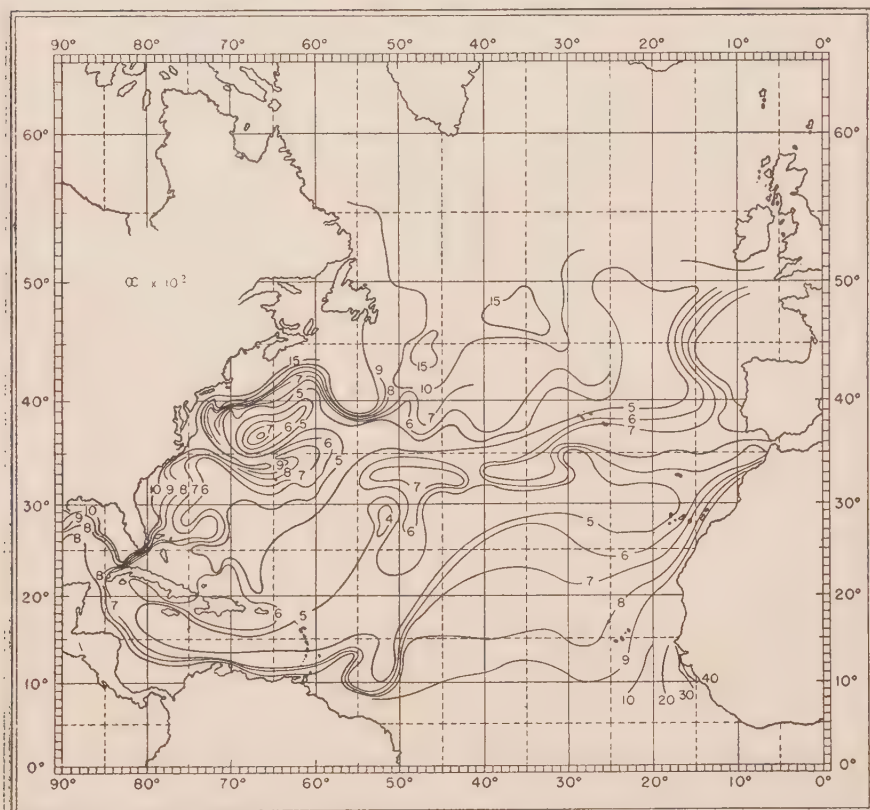


FIGURE 14.

to. These charts will require considerable revision when more observations are available. However, transparency like temperature, appears to be a characteristic of a water mass, and the close correspondence between the pattern in Figure 15 and that of temperature at a depth of 200 meters (Fuglister, *in litt.*) suggests that they are not grossly inaccurate. Charts of the depth distribution of 10^{-12} illumination at noon in mid-summer, were then prepared. This value, as in previous work, is based on a value of 100 arbitrary units at the surface with overhead sunlight. Finally, from available hydrographic data, charts of the distribution of T_{1-12} were prepared, as shown in Figures 17 and 18.



FIGURES 15, 16. Distribution of extinction coefficients. For simplicity, these are expressed as $\times 100$.

CORRELATION BETWEEN SPECIFIC ABUNDANCE AND TEMPERATURE

For the whole North Atlantic and Mediterranean, there were 165 localities for which both Euphausiid counts and the necessary temperature data were available. A graph was prepared for each Euphausiid species in which the ordinates were T_s and T_{1-12} . Each locality was entered on the graph according to its temperature, and with a notation of the percentage of the species in question at that station. The resulting graphs are unsuitable for reproduction here, but they are summarized in Figure 19. With the variation from one locality to another in the adequacy of the net hauls, perfect consistency is not to be expected. The areas contoured indicate the limits of conditions beyond which the species is almost always absent, and the conditions

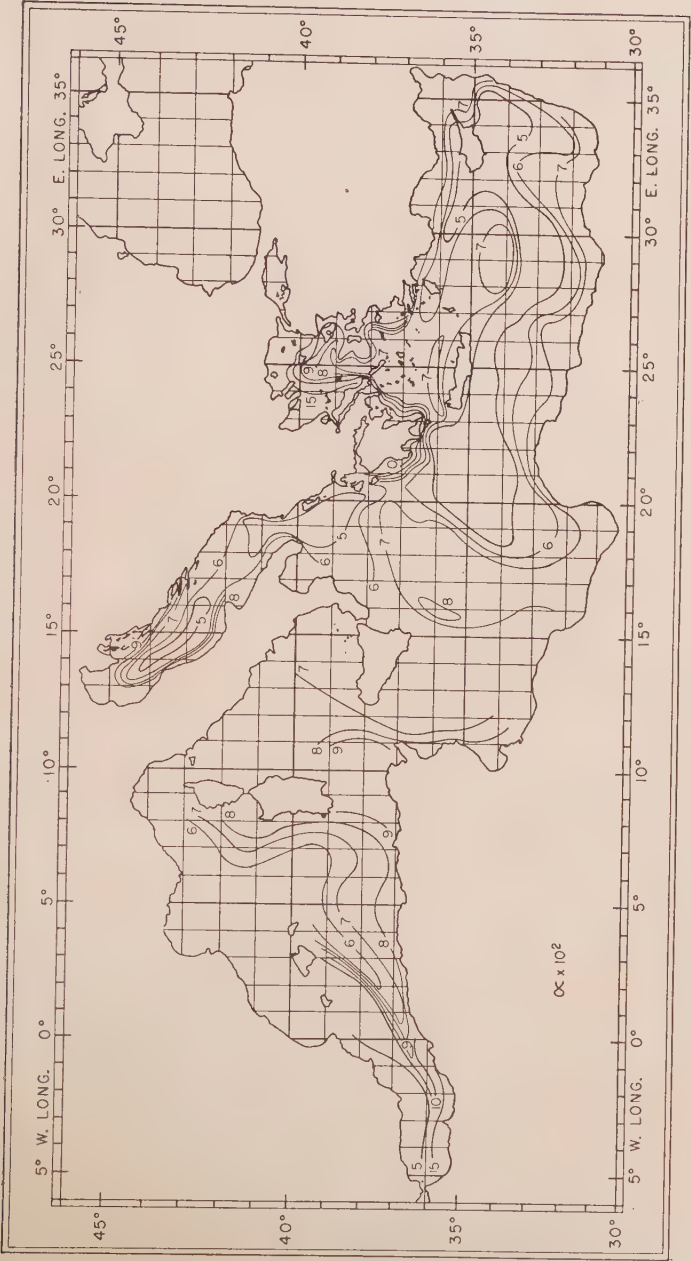
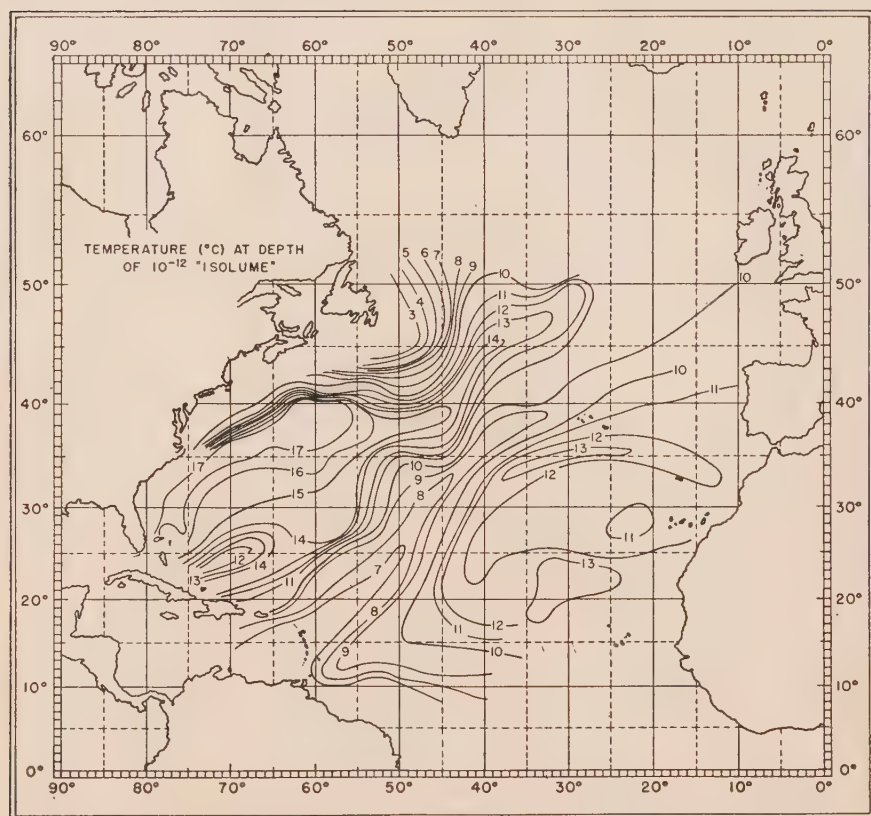


FIGURE 16.



FIGURES 17, 18. Distribution of temperature ($^{\circ}\text{C}.$) at the depth of 10^{-12} illumination in summer.

under which it is most abundant. The data do not warrant more exact classification than this. However, both the general shape of the contoured areas, and their marked specific differences are significant. It should be noted that the lower right area of each graph represents improbable hydrographic conditions where T_{1-12} approaches T_s in value, and from which observations are therefore lacking.

The absolute abundance of a given species is dependent, among other things, on the available food supply, and this varies considerably in different oceanic regions. The effect is eliminated by considering only the relative abundance of a species in the total Euphausiid population. If, at a given locality, conditions were optimal for only one species, then that species would dominate in the population. If several

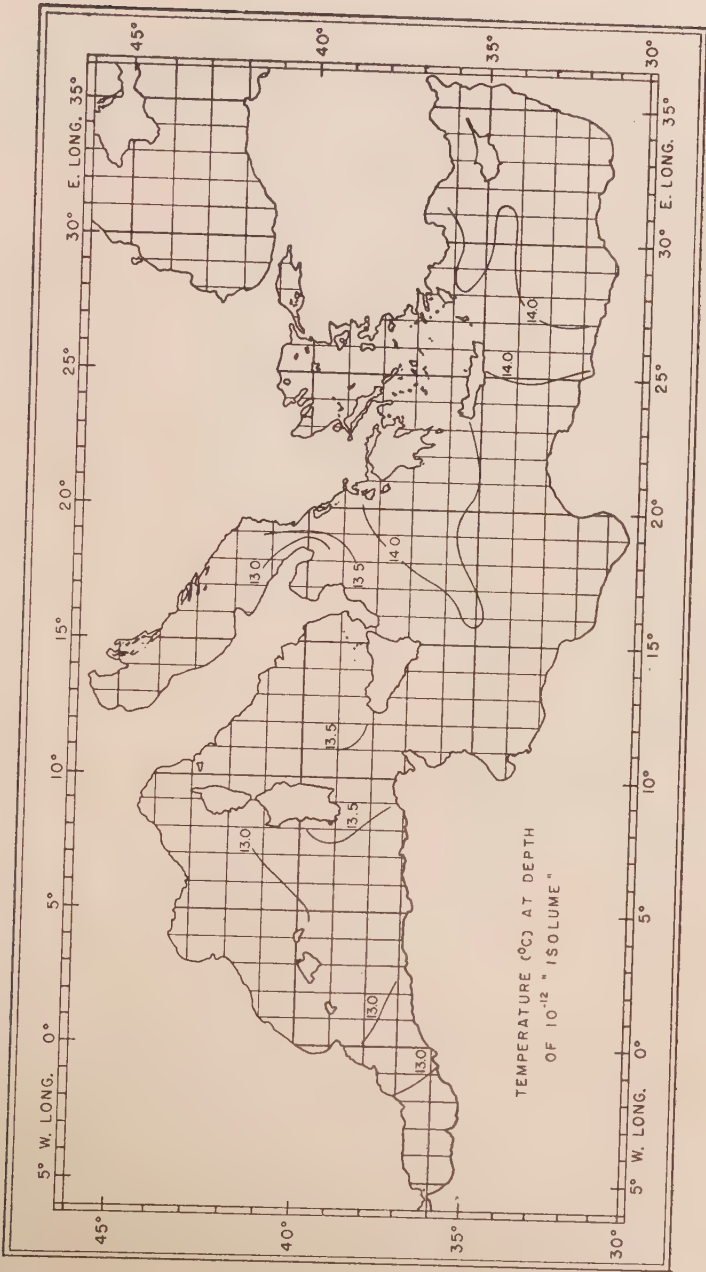


FIGURE 18.

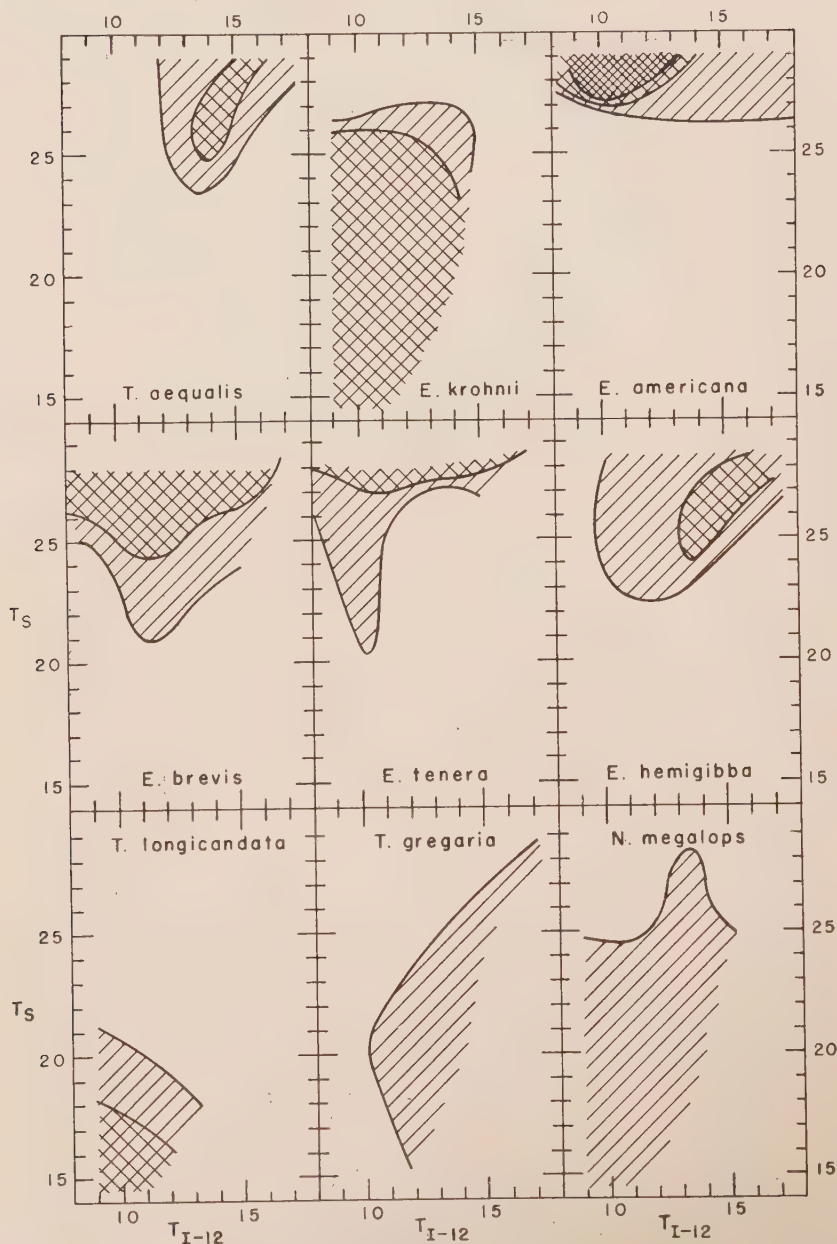


FIGURE 19. Relation between the abundance of the various species of Euphausiids, surface temperature and temperature at the depth of 10-12 illumination. Relative abundance indicated by depth of shading.

species found optimal conditions in the same locality, then each would be represented by a smaller percentage of the total population. Thus the contours shown in Figure 19 may represent not simply the degree to which various temperature conditions suit each species, but also the amount of competition from other species under these conditions. In a crude attempt to eliminate this latter effect, a second series of contours was produced, based on data in which the observed percentage of the species at each locality was multiplied by the number of competing species present there. As only minor modifications of the contours resulted, it was felt that the uncorrected contours might be taken as a reasonable representation of the relation of the abundance of each species to temperature. As such, it is legitimate to compare them with the theoretical patterns presented in Figures 2-4.

The observed temperature relations of *Thysanoessa gregaria* (Figure 19) might be matched by a relationship similar to that shown in Figure 2. In this case, the optimum temperature would be about 21°C. or higher and the tolerance range about $\pm 5^\circ$. Since the optimum appears to lie beyond the limit of our observations, it cannot be placed with any accuracy. It must be reiterated that the above statement does not imply that 21°C. is the optimum temperature for *T. gregaria*. The statement is that, under hydrographic conditions such that the summer maximum temperature at the surface, and also the temperature at the depth of 10^{-12} illumination in summer, both approach 21°, this species tends to be most abundant. Such conditions are unlikely to occur, and the abundance of this species reflects the departure of both T_s and T_{1-12} from this optimum. Furthermore, *T. gregaria* does not characteristically live either at the extreme surface at night or at the depth of 10^{-12} illumination in the daytime. In fact it appears to be a rather particularly deep living species, and one with a peculiarly variable day level.

Possibly *Thysanoessa longicaudata* shows a similar type of temperature relationship, but with a much lower optimum at about 11°C. This species was included solely to show a cold-water form for comparison, and its center of distribution lies in cold northern waters beyond those for which we have data, so no further attempt will be made to define its characteristics.

The remaining species, however, present a problem. They can all be matched, with greater or less exactness, by curves of the type shown in Figures 2-4. Thus *Euphausia brevis* and *E. tenera* approximate the pattern of Figure 3, in which there is a greater tolerance

range for temperatures below than for those above the optimum. *Euphausia hemigibba* and *Thysanopoda aequalis* more closely resemble the contours in Figure 4, in which an allowance is made for a degree of physiological adaptation. In none of these species, though, does a single temperature optimum meet the requirements. If, on the other hand, it is assumed that the optimum value of T_s is higher than that of T_{1-12} then good agreement is obtained.

It is true that the actual temperatures at the day and night levels of the species in question may not be as widely separated as the indicated values of T_s and T_{1-12} , but the implication still remains that there are different temperature optima at the day and night levels, and not a single optimum lying somewhere between the two. Furthermore, should it prove that temperature is not actually the operative factor, then the true factor would have to be one which is closely correlated with temperature, and as such showed two discrete optima. It is necessary, then, to justify the assumption of two temperature optima.

Allee, *et al.* (1949) state that "In the laboratory, organisms exposed to variable temperatures frequently, perhaps usually, show accelerated development as compared with those held at a constant temperature of the same value, if other conditions remain equal." They also point out that "the thermal optimum in the action of alternating temperatures may be different from the optimum for constant temperatures," and that "alternating temperatures may affect survival as well as the rate of development." Since different body processes differ in their optimum temperature, it might be expected that a fluctuating temperature, which allowed all the processes to enjoy optimum conditions for part of the time, might yield better results than any one fixed temperature which might be far removed from some of the optima. This is not a complete explanation, however, since work such as that of Parker (1930) has shown that exposure of grasshopper eggs to a temperature below that at which development takes place is followed by accelerated development when a higher temperature is resumed. It has been shown that spermatogenesis in many vertebrates has a lower optimum temperature than other body processes. There are more data available on limiting, than on optimum temperatures for such processes, but it appears that in such cases a fluctuating temperature is more favorable than a fixed one.

In the case of a diurnally migrating animal such as a Euphausiid, it is safe to assume that at least some of the body processes differ in the day and night habitats. The food supply is more abundant in the

night habitat. Increased feeding may, or may not imply more active swimming, but certainly involves more active masticatory and digestive processes. The evening ascent, involving extra energy expenditure, is into warmer water. Incidentally, if oxygen consumption increases with such increase in activity, the night levels favour this in having a higher oxygen concentration than the day levels. There is also a difference in water density of two to three thousandths between the two levels. While this is not great, the copepod *Calanus finmarchicus* has a density only about thirty thousandths greater than the sea water in which it occurs (Lowndes, 1942). If that is comparable with the density of a Euphausiid, then the density of the latter, relative to the water, and hence its sinking rate, must be at least several per cent higher at the night level than at the day level. It appears, then, that at least energy expenditure is different in the two habitats. We are not in a position, at present, to assess the relative advantages of a varying and a stable environment, but the possibility that there is a definite advantage to the animal in thus alternating its environments, is not unreasonable. It is tempting to speculate further that the importance of diurnal migration lies in the attainment of such alternation of temperature.

SPECIFIC TEMPERATURE RELATION CHARACTERISTICS

From Figure 19 it is now possible to characterize the optimum hydrographic conditions for the dominance of the different Euphausiid species. For *Thysanoessa longicaudata*, the optimum surface temperature lies below $14^{\circ}\text{C}.$, which is the limit included in the area here surveyed. For *T. gregaria* the value would be about $21^{\circ}\text{C}.$, and for *Nematoscelis megalops* and *Euphausia krohnii* perhaps the same, although the optimum is ill-defined. For *Euphausia hemigibba* and *Thysanoessa aequalis* the optimum is about $27^{\circ}\text{C}.$, while for *E. americana*, *E. brevis* and *E. tenera* it is $28^{\circ}\text{C}.$ or higher. T_{1-12} optimum is below $8^{\circ}\text{C}.$ for *Thysanoessa longicaudata*, and probably above $18^{\circ}\text{C}.$ for *T. gregaria*. It is fairly clearly defined at above $10^{\circ}\text{C}.$ for *E. americana*, $11^{\circ}\text{C}.$ for *E. brevis*, $15^{\circ}\text{C}.$ for *T. aequalis* and *E. hemigibba*. For *E. tenera* it is between about 10° and $15^{\circ}\text{C}.$, and for *N. megalops* it is ill-defined, but possibly about $13^{\circ}\text{C}.$ Finally, physiological adaptation appears to be more pronounced in *T. aequalis* and *E. hemigibba* than in the other species. *E. americana* is anomalous in that its tolerance range for T_{1-12} appears to be greater above the optimum than below. If the data supporting this are adequate, then the effect may be

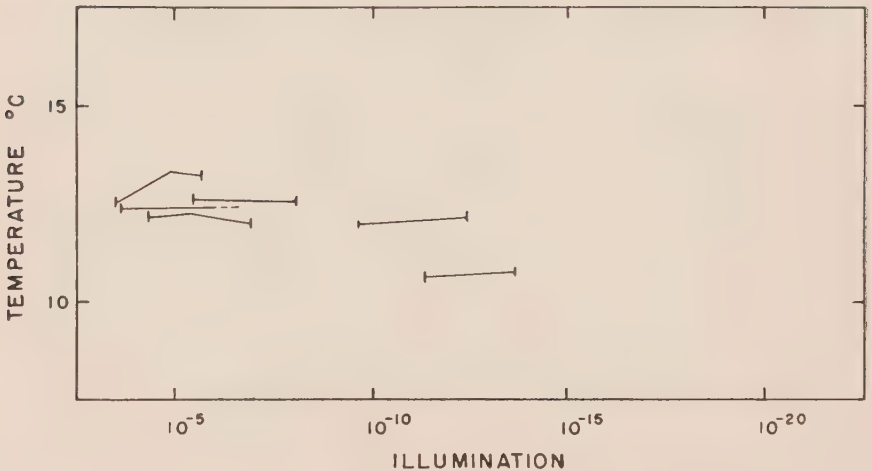


FIGURE 20. Data from a series of bathygrams showing the noon flattening period for what are believed to be pure populations of *Euphausia krohnii*. These show the conditions of temperature and illumination existing at the level of the scattering layer during the periods in question.

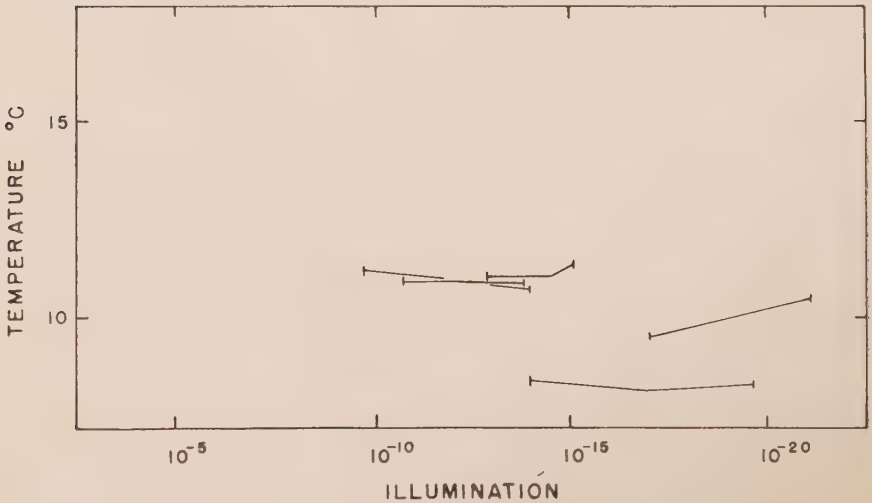


FIGURE 21. As in Figure 20, but for populations of *Nematoscelis megalops*.

genuine, but it may be that a factor other than temperature requires consideration here.

These values, as already emphasized, do not represent temperatures at the actual levels occupied by the Euphausiids. If the Euphausiid

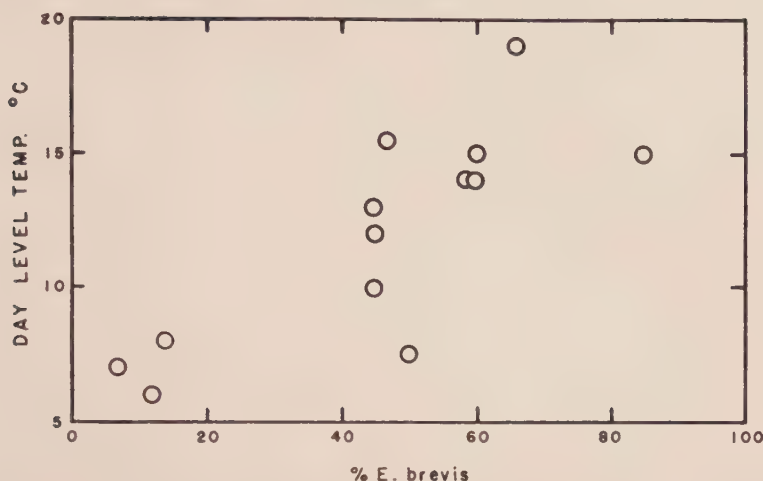


FIGURE 22. Correlation between the temperature at the level at which noon flattening occurs and the percentage of *Euphausia brevis* in the Euphausiid population.

origin of the phenomenon of the deep scattering layer be accepted, it is possible to obtain some information on critical temperatures at the actual depths concerned. A large proportion of the records of the day-time behaviour of this layer show periods of noon flattening which are interpreted as a change from illumination control to temperature control of depth. If the conditions of temperature and illumination under which this change-over occurs are compared with the composition of the local Euphausiid population, it should be possible to define certain characteristics of the different species. In the presence of a large number of species, each with its differing reaction characteristics, such an analysis is impossible, and unfortunately this applies to the areas from which we have most records. In an area to the north of the Azores, and also in part of the Mediterranean, there is a very simple population composed almost solely of *Euphausia krohnii* and *Nematoscelis megalops*. Where this is found, their record appears as two separate layers on the bathygrams. Figures 20 and 21 show a series of such records with only the noon flattening period included, plotted in terms of temperature and illumination. It will be seen that for *E. krohnii* the critical temperature at which descent is arrested is about 12°C., and for *N. megalops* it is lower, but less well defined. The illumination at which flattening commences varies widely, but is about 10^{-5} to 10^{-15} for *E. krohnii* and 10^{-10} to 10^{-20} for the deeper-

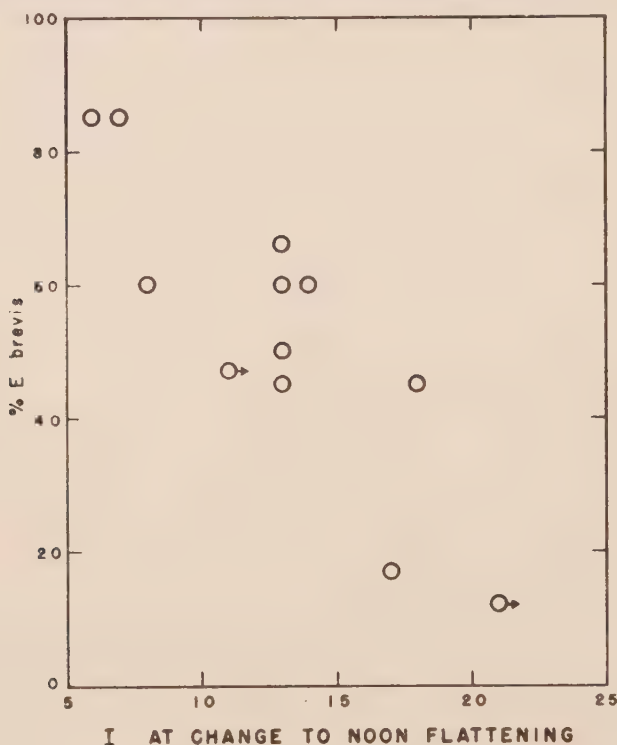


FIGURE 23. Correlation between the illumination at the level of the scattering layer at the time when descent ceases and noon flattening commences, and the percentage of *Euphausia brevis* in the Euphausiid population.

living *N. megalops*. The apparently greater illumination tolerance range of the latter cannot be considered significant since illumination changes more rapidly around noon at these greater depths.

Analysis is also possible for *Euphausia brevis*, since this is an abundant species, and the other species with which it occurs are believed to be all deeper-living. Figure 22 shows the correlation between the temperature at the depth of noon flattening and the percentage of *E. brevis* in the population, and Figure 23 shows the similar correlation of the illumination at the commencement of noon flattening. In both cases, decrease in the proportion of *E. brevis* and corresponding increase in the proportion of other, deeper-living species results in noon flattening occurring at a lower temperature and illumination. By extrapolation to a 100 per cent *E. brevis* population, it would

appear that this species descends at an illumination value of about 10^{-5} , and arrests descent at about $15-20^{\circ}\text{C}$. Figure 15 indicates optimum conditions for this species at about $T_{1-12} = 11-12^{\circ}\text{C}$. In the part of the North Atlantic where such conditions coincide with the indicated value to T_s , 10^{-5} illumination occurs at noon at a depth of 150-200 fathoms, at which depth the temperature is $15-18^{\circ}\text{C}$. It appears, then, that this species tends to arrest its descent at about the depth at which it encounters its optimum day temperature. Further, since Euphausids have been shown to be able to migrate vertically more than fast enough to maintain themselves at a constant illumination, it may be assumed that the level of illumination at which they are observed to descend is that best suited to them. If this is the case, then the data indicate that *E. brevis* is most successful, as indicated by its relative abundance, in those localities where the illumination at the level of noon flattening is close to that indicated as optimum during their period of descent.

PREDICTION OF GEOGRAPHICAL DISTRIBUTION FROM THEORETICAL TEMPERATURE RELATIONSHIPS

A further check on the dual optimum temperature control theory may be obtained by comparing the observed geographic distribution of a species with that predicted from theoretical curves and known hydrographic conditions. The values of the two temperature optima selected, and the type of relationship between departure from these optima and survival index, are those which are found by trial to suit a particular species most closely. Beyond this, the theoretical and observed distribution charts are arrived at from independent data. If a rather complicated distribution pattern can be reasonably well duplicated by the two methods, there is a strong probability that the limiting factors and their mechanism of control have been correctly chosen.

As an example, it has been assumed that the temperature relationship for *Euphausia hemigibba* is of the type shown in Figure 4, with asymmetrical temperature response and a degree of physiological adaptation. Such a diagram was prepared, based on the temperature optima indicated for the species, and with a fuller series of survival index contours. From this, and charts of the distribution of T_s and T_{1-12} , the distribution of survival index for the species for the North Atlantic was calculated. Since maximum values for this were 100 per cent and *E. hemigibba* rarely comprises more than a third

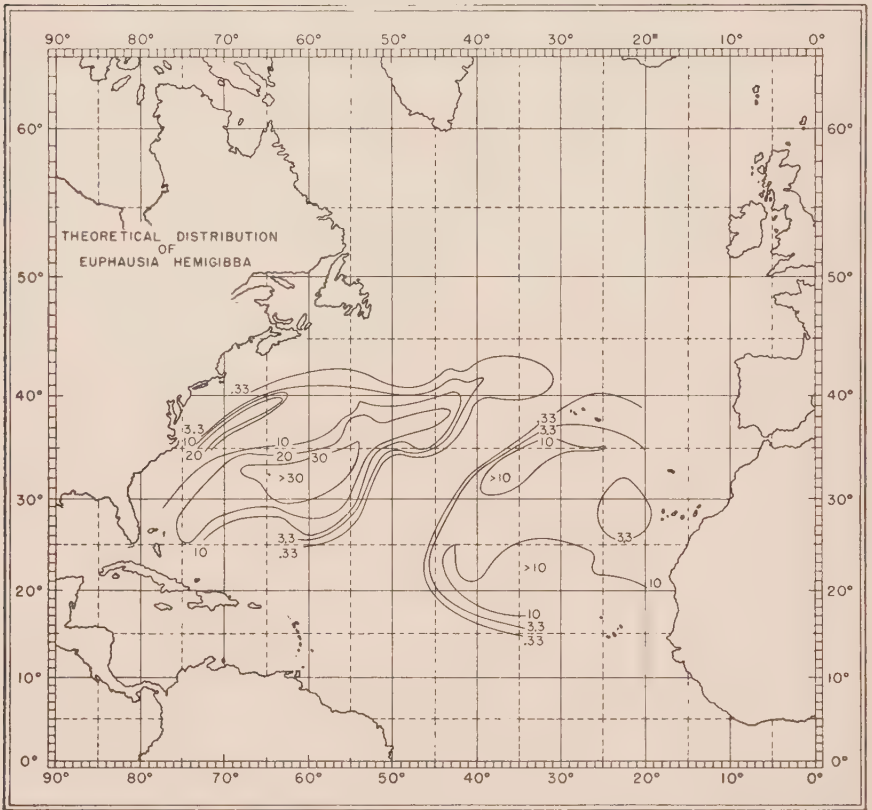


FIGURE 24. Predicted distribution of *Euphausia hemigibba* for comparison with the observed distribution shown in Figure 10. For explanation, see text.

of the total Euphausiid population, all values were divided by three to facilitate comparison with observed values. The results are shown in Figure 24, and should be compared with Figure 10. Considering the inadequacy of the net sampling in much of the area, and the over-simplified assumptions that have been made in the predicted distribution, the agreement between prediction and observation is good.

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